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The Regulation of Exogenous Jasmonic Acid on UV-B Stress Tolerance in Wheat

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Abstract Enhanced ultraviolet-B radiation (UV-B, 280–320 nm) is recognized as one of the environmental stress factors that cannot be neglected. Jasmonic acid (JA) is an important signaling molecule in a plant's defense against biotic and abiotic stresses. To determine the role of exogenous JA in the resistance of wheat to stress from UV-B radiation, wheat seedlings were exposed to 0.9 kJ m^{-2} h^{-1} UV-B radiation for 12 h after pretreatment with 1 and 2.5 mM JA, and the activity of antioxidant enzymes, the level of malondialdehyde (MDA), the content of UV-B absorbing compounds, photosynthetic pigments, and proline and chlorophyll fluorescence parameters were measured. The results of two-way ANOVA illustrated that the activities of superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT), MDA level, anthocyanin and carotenoid (Car) content, and almost all chlorophyll fluorescence parameters were significantly affected by UV-B, JA, and UV-B × JA ($P < 0.05$) [the maximal efficiency of photosystem II photochemistry (F_v/F_m) was not affected significantly by UV-B radiation]. Duncan's multiple-range tests demonstrated that UV-B stress induced a significant reduction in plant photosystem II (PSII) function and SOD activity and an increased level of membrane lipid peroxidation, indicative of the deleterious effect of UV-B radiation on wheat. JA pretreatment obviously mitigated the detrimental effect of UV-B on PSII function by increasing F_v/F_m, reaction centers' excitation energy capture efficiency (F_v'/F_m'), effective photosystem II quantum yield (ΦPSII), and photosynthetic electron transport rate (ETR), and by decreasing nonphotochemical quenching (NPQ) of wheat seedlings. Moreover, the activity of SOD and the content of proline and anthocyanin were provoked by exogenous JA. However, the MDA level was increased and Car content was decreased by exogenous JA with or without the presence of supplementary UV-B, whereas the contents of chlorophyll and flavonoids and related phenolics were not affected by exogenous JA. Meanwhile, exogenous JA resulted in a decrease of CAT and POD activities under UV-B radiation stress. These results partly confirm the hypothesis that exogenous JA could counteract the negative effects of UV-B stress on wheat seedlings to some extent.

Keywords Ultraviolet-B · Jasmonic acid · Chlorophyll fluorescence · Antioxidant enzyme · Plant hormone

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Introduction

Following the report about the Antarctic ozone hole by the British Antarctic Survey, the effect of enhanced ultraviolet-B (UV-B, 290–320 nm) radiation caused by the thinning ozone layer on plants attracted widespread concern

(Teramura 1990; Olszyk and others 1996; Rozema and others 1997; Yue and others 1998; Li and others 1999; Kakani and others 2003; Paul and Gwynn-Jones 2003; Qiu and others 2007; Li and others 2011). It has been acknowledged that UV-B radiation is only a small fraction (<1%) of the total solar spectrum, but it can have a major impact on plant growth and development. Enhanced UV-B radiation can be regarded as not only a factor in properly regulating plant physiological processes, but also a factor in the activation of the stress signal pathway, which results in plant cell damage and peroxidation (Worrest 1983; Holmes 2006; Gruber and others 2010; Rizzini and others 2011).

In the process of sensing internal and external environmental changes, regulating growth and development, and maintaining a proper state to adapt to adverse environmental stresses, plant hormones, as key signaling molecules, play an important role of mediating environmental signaling into the cell and the nucleus (Chung and others 2003). In recent years, plant hormones were considered a new way to improve plant stress tolerance, alleviate stress damage, and ensure the quality and yield of plants (crop) (Xu and Li 2006; Fedina and others 2009). Many studies showed that a plant's endogenous jasmonic acid (JA) content increased under biotic and abiotic stress conditions such as infection of pathogens, pests, and diseases, tissue damage (Kiribuchi and others 2005), drought (Anjum and others 2011; Takeuchi and others 2011), chilling (Ding and others 2001; Cao and others 2009), high salt (Fedina and Benderliev 2000; Takeuchi and others 2011), and light (Riemann and others 2003; Haga and Iino 2004; He and others 2005; Riemann and others 2008). As a consequence, defense gene expression for defense substance (defensive proteins, phenol, lignin, and proline) synthesis was induced and the stress resistance of plants was enhanced (Lorenzo and Solano 2005; Kiribuchi and others 2005; Hendrawati and others 2006; Wasternack 2007; Kim and others 2009; Shan and others 2009). It had been confirmed that JA and its metabolically active derivatives (jasmonates, JAs) are important signaling molecules involved in plant responses to biotic and abiotic stresses (McSteen and Zhao 2008). Some studies reported that exogenous JAs could improve the resistance of barley seedlings to salinity stress (Tsonev and others 1998; Yoon and others 2009; Takeuchi and others 2011), drought stress (Horton 1991; Irving and others 1992; Gao and others 2004; Takeuchi and others 2011), chilling injury (Cao and others 2009), and heat stress (Ding and others 2001) by increasing antioxidant enzyme activities and photosynthetic function, reducing stomatal conductance, enhancing water potential, lowering membrane permeability, increasing unsaturated fatty acid content, and some other means. As for UV-B stress, some studies showed that UV-B radiation defense signaling pathways might be regulated by endogenously synthesized JA. Conconi and others (1996) pointed out that in the plant response to UV-B radiation, the octadecanoid pathway for JA synthesis needed to be activated, and the mechanism was further confirmed by the employment of JA-sensitive *Arabidopsis* mutants (Mackerness and others 1999). However, little attention was paid to the influence of exogenous JA on plant UV-B resistance. As far as we know, only Zhang and Ervin (2005) and Fedina and others (2009) reported that exogenous jasmonic acid methyl ester (MeJA) could offset the effects of UV-B radiation by increasing the antioxidant defense of barley seedlings and Kentucky bluegrass.

The aim of this study was to evaluate the interactive effect of UV-B radiation and exogenous JA, ascertain the role of JA in the resistance to UV-B, and make clear the signal cross-talk between UV-B irradiation and JA at the physiological level using wheat seedlings.

Material and Methods

Plant Material

Uniform-sized wheat (*Triticum aestivum* cv. Shanbei 139) seeds were selected for the experiment. After surface sterilization for 10 min by 0.1% $HgCl_2$, the seeds were washed under flowing water for 30 min and then sown in glass culture dishes under white fluorescent lamps (300 μmol m^{-2} s^{-1}) with an 8/16-h light/dark cycle and a 25/20°C day/night temperature cycle. After germination, unwanted seedlings were removed. To minimize the effects of microenvironment variation, the position of each pot was changed daily.

JA Treatment

When the second pairs of leaves were fully expanded, some plants were sprayed with different concentrations of JA (Sigma-Aldrich Co., St. Louis, MO, USA), and then a part of the plants was subjected to UV-B radiation. Considering a preliminary concentration–response experiment, we chose the most appropriate JA concentration (1 and 2.5 mM) in this study.

UV-B Treatment

Additional UV-B radiation was supplied over 12 h via UV-B fluorescent lamps (36 W, Beijing Lighting Research Institute) following the procedure described in Qi and others (2002). The enhanced UV-B dose was 0.9 kJ m^{-2} h^{-1}; the radiation intensity was guaranteed by varying the distance between the lamp and the plant canopy. Immediately after

the end of the 12-h UV-B-radiation treatment, the youngest and most fully expanded leaves were collected, weighed, and then frozen in liquid nitrogen for later use.

The different treatments with JA and UV-B in this experiment are listed in Table 1.

Enzyme Activity Determination

Frozen laminas (0.1 g) were homogenized with a mortar and pestle with 5 ml of 50 mM ice-cold phosphate buffer (pH 7.8) containing 1 mM EDTA and 1% polyvinylpyrrolidone (PVP). The homogenate was centrifuged at 15,000×*g* for 15 min at 4°C. The supernatant was used for assays of superoxide dismutase (SOD) activity. SOD activity was analyzed by the method of Giannopolitis and Ries (1977) as described in Qiu and others (2008). Frozen laminas (0.20 g) were homogenized with a mortar and pestle with 2 ml of 50 mM ice-cold phosphate buffer (pH 7.8) containing 1 mM EDTA. The SOD activity was assayed by measuring its capacity to inhibit the photoreduction of nitroblue tetrazolium (NBT).

Frozen wheat leaf segments (0.1 g) were homogenized in 5 ml of 50 mM PBS (pH 7.0) containing 1 mM EDTA and 1% polyvinylpyrrolidone (PVP). The homogenate was centrifuged at 15,000×*g* for 15 min at 4°C. The supernatant was used for assays of catalase (CAT) and peroxidase (POD) activity. Catalase (CAT) activity was determined by the method of Cakmak and Marschner (1992). The decomposition of H_2O_2 was measured by following the decline in absorbance at 240 nm for 2 min. The 3-ml reaction mixture contained 50 mM phosphate buffer (pH 7.0), 15 mM H_2O_2, and 0.1 ml enzyme extract. The reaction was started with the addition of the enzyme extract. Absorbance at 240 nm was read every 30 s. One unit of catalase activity was defined as a change of 0.01 absorbance min^{-1} caused by the enzyme extract. Analysis of peroxidase (POD) capacity was based on oxidation of guaiacol using H_2O_2 according to the method of Nakano and Asada (1981) as described in Li and others (2011). The enzyme extract (0.02 ml) was added to the reaction mixture containing 0.02 ml guaiacol solution and 0.01 ml H_2O_2 solution in 3 ml of phosphate buffer solution (pH 7.0). Addition of the enzyme extract started the reaction, and the increase in absorbance was recorded at 470 nm for 5 min. Enzyme activity was quantified by the amount of tetraguaiacol formed using its molar extinction coefficient.

Malondialdehyde (MDA) Determination

Malondialdehyde (MDA) concentration was determined by the method of Qiu and others (2008) with some modification. Samples of leaves [0.10 g fresh weight (FW)] were homogenized in 50 mM phosphate buffer (pH 7.8) and then centrifuged for 15 min at 8,000×*g*. A 1-ml supernatant sample was combined with 2 ml thiobarbituric acid (TBA) reagent and heated at 100°C for 20 min, chilled on ice, and then centrifuged at 10,000×*g* for 5 min. To remove the disturbance of soluble sugar and anthocyanin in the sample (absorbance at 450 and 532 nm, respectively), the amount of MDA was calculated using the formula: $C = 6.45 \times (A_{532}–A_{600})–0.56 \times A_{450}$, where C is the concentration of MDA in the supernatant and A_{532}, A_{600}, and A_{450} are the absorbance values at 532, 600, and 450 nm, respectively. The MDA concentration was finally expressed as mmol g^{-1} FW.

Proline Determination

The proline content was estimated using the method of Bates and others (1973). The plant material was homogenized in 3% aqueous sulfosalicylic acid and the homogenate was centrifuged at 10,000 rpm. The supernatant was used for estimation of proline content. The reaction mixture consisted of 2 ml supernatant, 2 ml acid ninhydrin, and 2 ml of glacial acetic acid, which was boiled at 100°C for 1 h. After termination of the reaction in the ice bath, the reaction mixture was extracted with 4 ml of toluene and the absorbance was read at 520 nm.

UV-B-Absorbing Compound Determination

The UV-B-absorbing compound content was assessed on whole-lamina extracts with spectroscopy using the method

Table 1 The different treatments conducted in this study

Treatment group	Interpretation
CK	Control
JA1	JA control group-1: seedlings were sprayed with 1 mM JA
JA2.5	JA control group-2.5: seedlings were sprayed with 2.5 mM JA
UV-B	Seedlings were treated with 12 h of UV-B radiation
UV-B + JA1	Seedlings were sprayed with 1 mM JA before additional 12 h of UV-B radiation
UV-B + JA2.5	Seedlings were sprayed with 2.5 mM JA before additional 12 h of UV-B radiation

of Teklemariam and Blake (2003) with some modifications. A 0.15-g sample was used for UV-B-absorbing compound concentration analysis. Samples were placed in 100-ml Erlenmeyer flasks containing methanol, HCl, and distilled H_2O (79:1:20 v/v/v) for 24 h. The total concentration of flavonoids and related phenolics were estimated by measuring absorbance at 300 nm and anthocyanin at 535 nm, according to Nogués and others (1998), with a UV/visible spectrophotometer (Lambda35, PerkinElmer, Waltham, MA, USA).

Photosynthetic Pigment Determination

The photosynthetic pigments of seedling leaves were extracted with 10 ml of 80% acetone. The content of chlorophyll *a* (Chl *a*), chlorophyll *b* (Chl *b*), and carotenoid (Car) were measured according to Lichtenthaler and Buschmann (2001).

Measurements of Chlorophyll Fluorescence Parameters

After 30 min of adaptation to the dark, the chlorophyll fluorescence parameters were measured with a LI-6400 portable photosynthesis system (LI-COR, Lincoln, NE, USA) with a fluorescence chamber. The minimal fluorescence yield (F_0) was determined by measuring the modulated light that was sufficiently low (<0.1 μmol m^{-2} s^{-1}) so as not to induce any significant variable fluorescence, and the maximal fluorescence yield (F_m) determined by a 0.8-s saturating pulse at 10,000 μmol m^{-2} s^{-1} in dark-adapted leaves. The leaves were then continuously illuminated with white actinic light at an intensity of 600 μmol m^{-2} s^{-1} for about 10 min. The steady-state value of fluorescence (F_s) was recorded thereafter, and a second saturating pulse at 10,000 μmol m^{-2} s^{-1} was imposed to determine the maximal fluorescence level in light-adapted leaves (F_m'). In both dark- and light-adapted states, the fluorescence parameters were expressed using the following formulae (van Kooten and Snel 1990): (1) the maximal efficiency of photosystem II (PSII) photochemistry, $F_v/F_m = (F_m–F_0)/F_m$; (2) the actual PSII efficiency, $\Phi PSII = (F_m–F_s)/F_m$; (3) the photosynthetic electron transport rate (ETR) was estimated after Krall and Edwards (1992) by multiplying ΦPSII × incident PPFD by 0.5 (two photons were used for exciting one electron because we had assumed an equal distribution of excitation between PSII and PSI), and by 0.84, which was considered the most common leaf absorbance coefficient for C3 plants (Björkman and Demmig 1987); (4) photochemical quenching, $qP = (F_m'–F_s')/(F_m'–F_0')$; (5) The Stern–Volmer NPQ was calculated using the expression $NPQ = (F_m–F_m')/F_m'$.

Statistical Analyses

A two-way analysis of variance (ANOVA) and Duncan's multiple-range test were performed to investigate the effects of exogenous JA and UV-B on the physiological parameters of seedlings at 0.05 probability levels using STATISTICA 6.0 software (StatSoft Inc., Tulsa, OK, USA).

Results

The effects of UV-B, JA, and their interaction (UV-B × JA) in terms of activity of antioxidant enzymes, content of MDA, proline, UV-B-absorbing compounds, and photosynthetic pigments and chlorophyll fluorescence parameters are presented in Table 2 according to a two-way ANOVA.

Antioxidant Enzyme Systems

Antioxidant enzyme activities (SOD, POD, and CAT) were affected significantly by UV-B, JA, and UV-B × JA ($P < 0.001$) (Table 2). Figure 1 shows that exposure of wheat seedlings to UV-B radiation resulted in a significant reduction of SOD activity by almost half, although it induced elevation of POD and CAT activity by 77 and 67%, respectively ($P < 0.05$). The effect of JA pretreatment alone on antioxidant enzymes depended on the concentration of JA; for example, SOD and POD activity could be improved by 13–56%, respectively, under 2.5 mM JA pretreatment ($P < 0.05$), and CAT activity was enhanced by 27% with 1 mM JA ($P < 0.05$). The combination of UV-B and JA resulted in a 35 and a 58% increase in SOD activity (1 and 2.5 mM JA, respectively) compared to the UV-B-exposed group ($P < 0.05$); nevertheless, the increase was still lower than that of CK. In contrast, the combination of UV-B and JA depressed the CAT and POD activity significantly compared with UV-B treatment alone; despite that, it maintained a higher level of CAT and POD activity than that of CK ($P < 0.05$, Fig. 1).

MDA

The MDA level was significantly affected by UV-B, JA, and their interaction ($P < 0.001$) (Table 2). As shown in Fig. 2, UV-B and JA alone had the same effect on MDA content and the highest MDA level was observed in the UV-B + JA_1 group.

Proline

The proline content was significantly affected by UV-B and UV-B × JA, especially by UV-B radiation

Table 2 Effects of UV-B, JA, and their interaction (UV-B × JA) for the parameters considered by two-way analysis of variance (ANOVA)

Dependent variable	Independent variable		
	UV-B	JA	UV-B × JA
F_0	47.070***	14.986***	5.076*
F_m	259.060***	52.087***	25.064***
F_v/F_m	1.800 ns	695.400***	36.600***
ΦPSII	25.941***	198.765***	29.824***
F_v'/F_m'	81.000***	458.111***	25.000***
qP	26.889***	190.889***	10.889**
ETR	19.031***	179.500***	28.643***
NPQ	345.316***	159.158***	61.263***
CAT	270.660***	164.224***	42.483***
POD	604.864***	87.728***	694.778***
SOD	146.964***	464.948***	418.136***
Flavonoids and related phenolics	0.097 ns	4.308**	0.353 ns
Anthocyanin	71.994***	17.077***	13.379***
MDA	67.587***	29.624***	18.678***
Pro	116.742***	6.015*	6.254*
Chl *a*	0.199 ns	1.678 ns	3.725 ns
Chl *b*	0.869 ns	4.738*	2.221 ns
Chl *a/b*	0.186 ns	2.800 ns	1.480 ns
Car	40.022***	17.641***	13.151***

Numbers represent *F* values at 5% level

Ns not significant

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

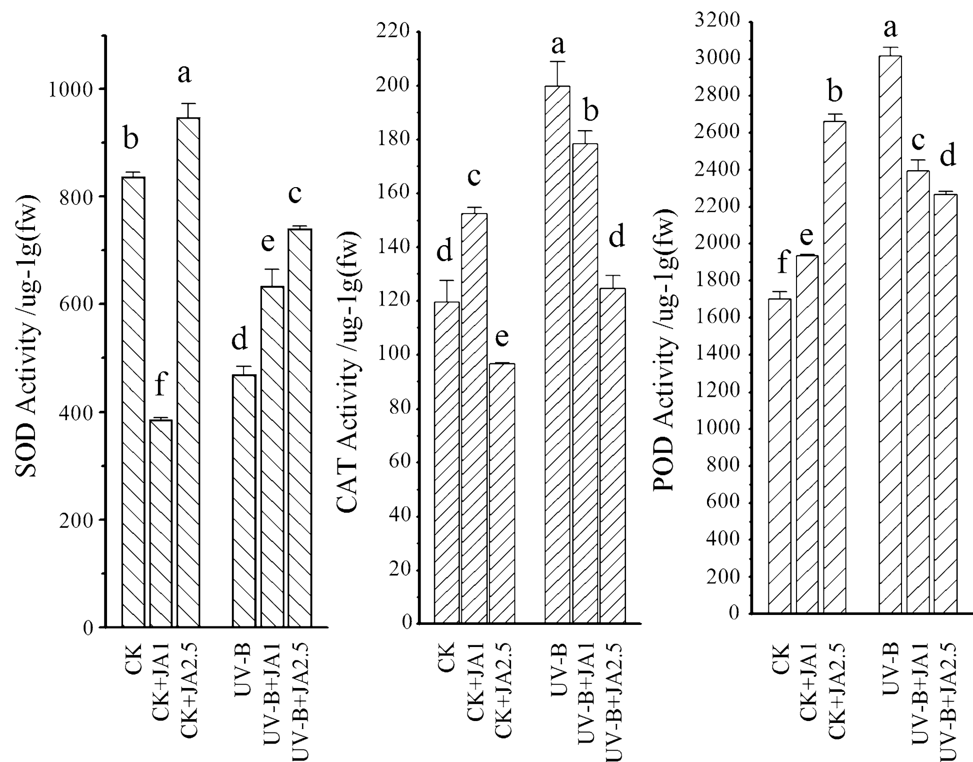

Fig. 1 Activity of SOD, CAT, and POD in the leaves of wheat seedling after JA and 12-h UV-B-irradiation treatment. CK, the control; JA1, seedlings were sprayed with 1 mM JA; JA2.5, seedlings were sprayed with 2.5 mM JA; UV-B, seedlings were treated with 12 h of UV-B radiation; UV-B + JA1, seedlings were sprayed with 1 mM JA before additional 12 h of UV-B radiation; UV-B + JA2.5, seedlings were sprayed with 2.5 mM JA before additional 12 h of UV-B radiation. Different letters indicate significant difference among treatments at the 0.05 significance level based on Duncan's multiple-range test. *Error bars* indicate standard error of the mean ($n = 3$)

($P < 0.001$, Table 1). Compared with CK, JA treatment alone did not influence proline content, but UV-B irradiation increased the proline level by 39% ($P < 0.05$), and the combination of 2.5 mM JA and UV-B radiation led to an increase in proline content of about 78% ($P < 0.05$), even higher than that of the UV-B group (Fig. 2).

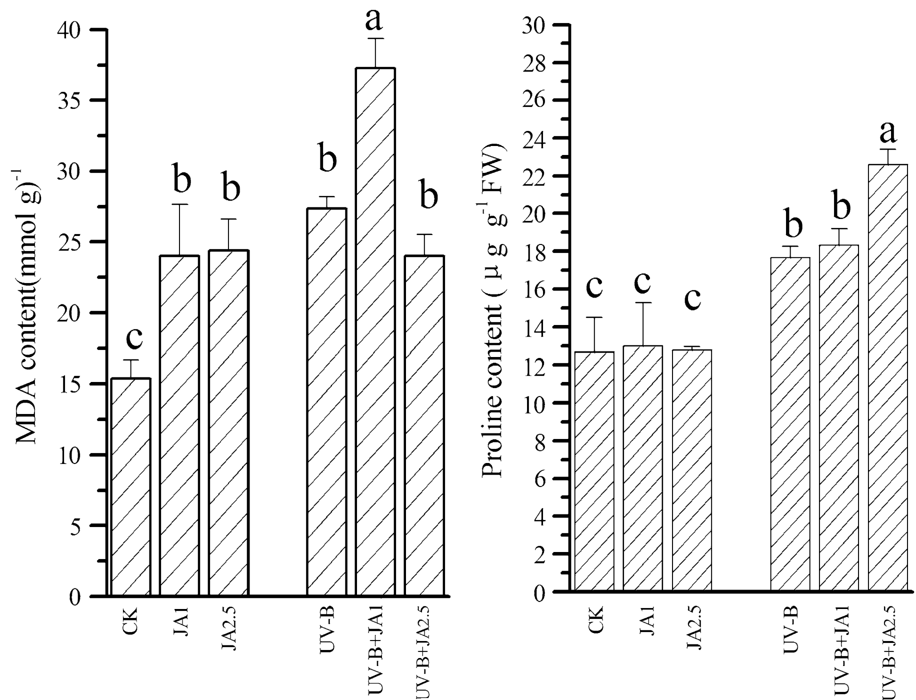

Fig. 2 MDA and proline content in the leaves of wheat seedling after JA and 12-h UV-B-irradiation treatment. CK, the control; JA1, seedlings were sprayed with 1 mM JA; JA2.5, seedlings were sprayed with 2.5 mM JA; UV-B, seedlings were treated with 12 h of UV-B radiation; UV-B + JA1, seedlings were sprayed with 1 mM JA before additional 12 h of UV-B radiation; UV-B + JA2.5, seedlings were sprayed with 2.5 mM JA before additional 12 h of UV-B radiation. *Different letters* indicate significant difference among treatments at the 0.05 significance level based on Duncan's multiple-range test. *Error bars* indicate standard error of the mean ($n = 3$)

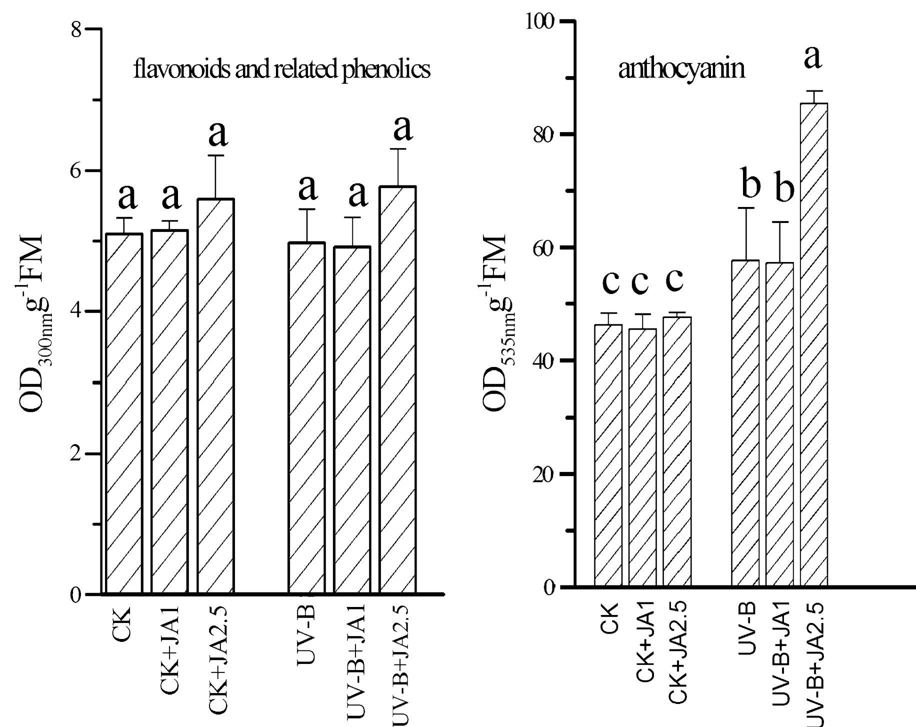

Fig. 3 Content of flavonoids and related phenolics and anthocyanin in the leaves of wheat seedling after JA and 12-h UV-B-irradiation treatment. CK, the control; JA1, seedlings were sprayed with 1 mM JA; JA2.5, seedlings were sprayed with 2.5 mM JA; UV-B, seedlings were treated with 12 h of UV-B radiation; UV-B + JA1, seedlings were sprayed with 1 mM JA before additional 12 h of UV-B radiation; UV-B + JA2.5, seedlings were sprayed with 2.5 mM JA before additional 12 h of UV-B radiation. Different letters indicate significant difference among treatments at the 0.05 significance level based on Duncan's multiple-range test. *Error bars* indicate standard error of the mean ($n = 3$)

UV-B-Absorbing Compounds

As shown in Table 2, the anthocyanin content was significantly affected by JA, UV-B, and UV-B × JA ($P < 0.001$), although flavonoids and related phenolics content was influenced significantly only by JA alone ($P < 0.01$). Figure 2 demonstrated that UV-B alone and in combination with JA promoted anthocyanin content significantly; however, JA alone and JA × UV-B had no significant influence

on the level of flavonoids and the related phenolics statistically compared to the UV-B group (Fig. 3).

Photosynthetic Pigments

UV-B alone and in combination with JA had no significant effect on the level of Chl *a* and Chl *a/b* statistically. The Chl *b* content was affected by JA alone significantly ($P < 0.05$), whereas the content of Car was affected by three treatments (JA, UV-B, and UV-B × JA) significantly ($P < 0.001$) (Table 2). The 2.5-mM-JA pretreatment induced an increase in Chl *a* and Chl *b* levels and a decrease in Car content ($P < 0.05$, Fig. 4). UV-B and exogenous JA had no significant effect on Chl *a*, Chl *b*, and Chl *a/b* in wheat seedlings, whereas 12-h UV-B exposure resulted in a decline in Car content, and exogenous JA made this trend even more dramatic (Fig. 4).

Chlorophyll Fluorescence

In the present experiment, JA, UV-B, and UV-B × JA had an obvious effect on chlorophyll fluorescence parameters

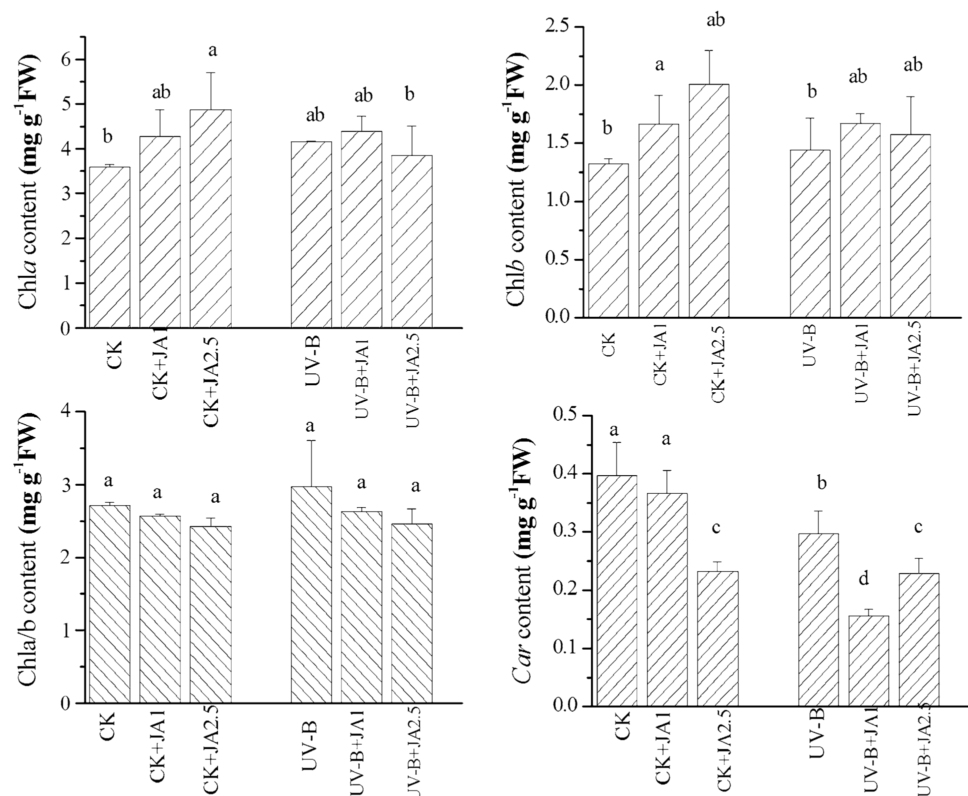

Fig. 4 Chloroplast pigment content in the leaves of wheat seedling after JA and 12-h UV-B-irradiation treatment. CK, the control; JA1, seedlings were sprayed with 1 mM JA; JA2.5, seedlings were sprayed with 2.5 mM JA; UV-B, seedlings were treated with 12 h of UV-B radiation; UV-B + JA1, seedlings were sprayed with 1 mM JA before additional 12 h of UV-B radiation; UV-B + JA2.5, seedlings were sprayed with 2.5 mM JA before additional 12 h of UV-B radiation. *Different letters* indicate significant difference among treatments at the 0.05 significance level based on Duncan's multiple-range test. *Error bars* indicate standard error of the mean ($n = 3$)

Table 3 Chlorophyll fluorescence parameters of wheat seedling after JA and 12 h of UV-B irradiation treatment

Treatment group	CK	JA1	JA2.5	UV-B	UV-B + JA1	UV-B + JA2.5
F_0	47.30 ± 1.39b	51.48 ± 2.45a	49.23 ± 0.08ab	41.87 ± 1.08c	45.10 ± 1.32b	47.65 ± 0.79b
F_m	236.31 ± 2.09b	253.18 ± 3.90a	237.13 ± 2.97b	206.42 ± 1.50d	223.39 ± 3.74c	228.60 ± 2.90c
F_v/F_m	0.50 ± 0.01e	0.61 ± 0.01a	0.52 ± 0.01d	0.49 ± 0.01f	0.60 ± 0.01b	0.54 ± 0.01c
F_v'/F_m'	0.49 ± 0.00cd	0.59 ± 0.01a	0.50 ± 0.01c	0.43 ± 0.02e	0.57 ± 0.00b	0.48 ± 0.00d
ΦPSII	0.39 ± 0.01b	0.46 ± 0.01a	0.39 ± 0.01b	0.32 ± 0.02c	0.47 ± 0.01a	0.39 ± 0.01b
qP	0.51 ± 0.01d	0.61 ± 0.01b	0.51 ± 0.01d	0.57 ± 0.02c	0.63 ± 0.01a	0.51 ± 0.01d
NPQ	0.28 ± 0.01d	0.34 ± 0.01c	0.26 ± 0.01d	0.44 ± 0.01a	0.39 ± 0.01b	0.27 ± 0.02d
ETR	17.63 ± 0.09b	23.45 ± 0.20a	19.54 ± 0.08b	16.30 ± 1.16b	23.87 ± 0.31a	19.60 ± 0.39b

CK = the control; JA1 = seedlings were sprayed with 1 mM JA; JA2.5 = seedlings were sprayed with 2.5 mM JA; UV-B = seedlings were treated with 12 h of UV-B radiation; UV-B + JA1 = seedlings were sprayed with 1 mM JA before additional 12 h of UV-B radiation; UV-B + JA2.5 = seedlings were sprayed with 2.5 mM JA before additional 12 h of UV-B radiation

Data are expressed as mean values ± SE. Different *letters* indicate significant difference between treatments at the 0.05 significance level based on Duncan's multiple-range test

(F_0, F_m, ΦPSII, F_v'/F_m', qP, ETR, and NPQ), except for F_v/F_m according to a two-way ANOVA at the 0.05 level (Table 2). Table 3 shows that the minimal fluorescence yield (F_0), maximal fluorescence level (F_m), maximal photochemical efficiency (F_v/F_m), excitation energy capture efficiency of PSII reaction centers (F_v'/F_m'), and effective PSII quantum yield (ΦPSII) decreased as the result of UV-B treatment. By contrast, qP and NPQ were increased under UV-B stress, and UV-B radiation had no significant effect on ETR (Table 3). Application of exogenous JA improved these parameters comprehensively. Accordingly, under UV-B exposure, JA-sprayed seedlings exhibited higher levels of the fluorescence parameters compared to the control group.

Discussion

Antioxidative Enzymes, Membrane Lipid Peroxidation, and Proline

It was well known that when plants were subjected to environmental stress, the balance between the production of reactive oxygen species (ROS) and the quenching activity of antioxidants was upset and this often resulted in oxidative damage (Furtana and Tipirdamaz 2010). Also, many studies have proven that UV-B-generated ROS will result in oxidative stress in plant cells (Qiu and others 2007; Li and others 2011). Concomitantly, transcripts of key antioxidative enzymes such as SOD, POD, and CAT were also induced under exposure to UV-B irradiation, and SOD acted as the first line of defense against ROS. SOD detoxified superoxide anion free radicals by forming H_2O_2; it could be further eliminated by the concerted action of CAT and POD (Kumari and others 2006; Yang and others 2007; Singh and others 2011).

Our data showed that 1 mM JA alone and UV-B radiation alone inhibit SOD activity, and that the combination of UV-B and 1 mM JA has a smaller inhibitory effect. This result may be caused by the antagonistic effect of UV-B and JA. Exogenous JA pretreatment could make up the loss of SOD activity caused by UV-B stress, although it did not reach the level of the control. Similar results were reported in 12-day-old barley seedlings treated with MeJA (Popova and others 2003), in peanut seedlings treated with JA (Kumari and others 2006), in rice seedlings under salt stress (Moons and others 1997), and in bluegrass under UV-B stress (Zhang and Ervin 2005).

In addition, although the combination of UV-B and JA depressed CAT and POD activity significantly compared with UV-B treatment alone, it maintained a higher activity of CAT and POD than that of CK. The results were different with barley and bluegrass treated by MeJA under UV-B stress (Zhang and Ervin 2005; Fedina and others 2009); that difference was related to the effect of the various concentrations of JAs used in the experiments. Exogenous JA was often used to imitate infection by pathogens, pests, and diseases; the tissue damage had similar effects on plants (Kiribuchi and others 2005; Wasternack 2007). Under those conditions, excessive ROS were produced and the level of antioxidant enzyme activity was elevated. Therefore, JA could beforehand provoke the antioxidative defense system of seedlings so as to defend against UV-B stresses to some extent (Anjum and others 2011).

On the other hand, UV-B irradiation resulted in the perturbation of plant membranes and/or the activation of lipases (Fedina and others 2009). MDA is produced when polyunsaturated fatty acids in the membrane undergo peroxidation. In the present experiments, the content of MDA increased under UV-B stress and JA treatment alone; the combination of UV-B and 1 mM JA resulted in even higher levels of MDA, but 2.5 mM JA pretreatment could slightly alleviate the lipid peroxidation caused by UV-B stress. Regardless of the improvement of membrane stability by MeJA under stress revealed by Popova and others (2003), the enhancement of MDA after application of JA was reported by many researchers (Fedina and Benderliev 2000; Kumari and others 2006), just as in this study.

From a quantitative point of view, proline has multiple functions such as osmotic pressure regulation, protection of membrane integrity, stabilization of enzymes/proteins, maintenance of appropriate $NADP^+/NADPH$ ratios, and scavenging of free radicals (Hare and Cress 1997). Accumulation of proline under stress conditions, for example, high salinity, high photosynthetic photon flux, and jasmonic acid presence in plants, has been correlated with stress tolerance (Ali and others 2007). In our research, we found that exogenous JA could improve tolerance to UV-B by increasing the content of proline, and that related alterations in proline metabolism might impinge on systems of redox control of plant gene expression (Hare and Cress 1997). Similar results were recorded with barley seedlings by exogenous MeJA under UV-B stress (Fedina and others 2009).

Secondary Metabolites

Many studies have reported that UV-B induced an increased level of secondary metabolites, which could counteract UV-B stress or indirectly protect plants via suppression of ROS and reduction of oxidative damage (Du and others 2011). Also, JA had been shown to stimulate secondary metabolite accumulation (stilbene, anthocyanin, and β-carotene) and to increase the synthesis of alkaloids, terpenoids, and phenolics (Wang and others 2008; Morales

and others 2010). In this study, flavonoids and related phenolics were not significantly affected by UV-B and JA treatment, whereas treatments of UV-B alone and in combination with JA, especially the combination of UV-B and 2.5 mM JA ($P < 0.05$), had significant promotional effects on anthocyanin content. The accumulation of flavonoids and related phenolics was often proposed as an adaptive mechanism to prevent radiation from reaching the mesophyll (Indrajith and Ravindran 2009); in addition, anthocyanins had the potential to mitigate photooxidative injury in leaves by shielding chloroplasts from excess high-energy quanta and by scavenging reactive oxygen species (Neill and Gould 2003). External use of JAs led to an increase in anthocyanin content in many plants (Shan and others 2009), and it was speculated that JA-specific F-box protein COI1 could induce expression of the "late" anthocyanin biosynthetic genes *DFR*, *LDOX*, and *UF3GT* (Shan and others 2009). Anthocyanins, along with other flavonoids and related phenolics, could directly scavenge molecular species of active oxygen, including hydrogen peroxide, singlet oxygen, and the superoxide hydroxyl, and peroxyl radicals (Gould and others 2002).

The effect of JAs on chloroplast pigments had been reported frequently. For example, mRNA of AtCLH1 involving chlorophyll degradation was inducible by MeJA (Tsuchiya and others 1999). On the other hand, some experiments had various observations; Kovač and Ravnikar (1994) reported the opposite influence of JA on the photosynthetic pigment content of two potato varieties. Our study showed that 2.5 mM JA alone led to a significant increase in Chl *a* and *b*, a decrease of Car, and uniformity of Chl *a/b*. Under UV-B irradiation, the Car level was also decreased by JA pretreatment, with the result similar to that reported by Fedina and others (2009).

Chlorophyll Fluorescence Parameters

The inhibited effect of elevated UV-B radiation on plant photosynthesis had been demonstrated by many investigators (see review by Kakani and others 2003). Meanwhile, PSII was considered the most sensitive component of the photosynthetic apparatus to UV-B exposure (Yang and others 2007). Chlorophyll fluorescence quenching analysis was used continuously to monitor the responses of photosynthetic apparatus to environmental stress, and PSII function can be assessed by using the fluorescence parameters of maximal photochemical efficiency (F_v/F_m), reaction centers' excitation energy capture efficiency (F_v'/F_m'), effective PSII quantum yield (ΦPSII), and the photosynthetic electron transport rate (ETR) (Wen and others 2005; Gao and Zhang 2008). In the present study, the fluorescence data also showed the adverse effect of UV-B stress on PSII function, for instance, the suppression of F_v/F_m, F_v'/F_m', ΦPSII, and ETR, which had been recorded by many researchers (Yang and others 2007; Szôllôsi and others 2008). In addition, the decline of F_m was observed under UV-B exposure, which was the result of damage to PSII reaction center proteins impacted by UV-B radiation, and the nonfunctioning PSII reaction centers start to act as quenching centers, which means a lowering of F_m for the total population (Krause and Weis 1988). In addition, accompanied by the promotion of donor-side photoinhibition caused by UV-B radiation, strongly oxidizing species of donor-side could possibly induce the formation of an oxidized β-carotene that might act as a fluorescence quencher (Allakhverdiev and others 1997).

Although PSII function was injured by UV-B radiation, JA pretreatment could remedy the damage caused by UV-B radiation and even enhance the PSII function of F_v/F_m, F_v'/F_m', ΦPSII, and ETR. This kind of promotional effect of JAs on the stressed plant's photosynthesis ability had been observed in other plants such as pear leaves under drought stress (Gao and others 2004).

The UV-B-radiation-induced inhibition of PSII photochemistry would result in excessive excitation energy, which would damage PSII due to over reduction of reaction centers if it could not be dissipated in a timely manner (Yang and others 2007). Thermal dissipation of excitation energy was described as nonphotochemical quenching (NPQ) of chlorophyll fluorescence. It helped to regulate and protect photosynthesis in environments in which light energy absorption exceeded the capacity for light utilization. Xanthophyll cycle pigments were known as allosteric effectors of NPQ and were dependent mainly on the process of violaxanthin de-epoxidation (Müller and others 2001). Yet, changed tendencies of NPQ under UV-B stress were recorded in different plants. Moon and others (2011) had documented NPQ suppression by UV-B irradiation, discriminating among cucumber, tomato, and *Arabidopsis*. They reported that NPQ suppression should correlate with a marked decrease in photosynthetic electron transport more than xanthophyll cycle enzymes. In our study, 12 h of UV-B radiation induced a 57% increase of NPQ ($P < 0.05$) and a 7.54% decrease of ETR, which was consistent with the results determined in other plants such as beech seedling and sessile oak under UV-B stress (Láposi and others 2005; Szôllôsi and others 2008). Exogenous JA pretreatment, however, especially 1 mM JA, might further enhance the promotion of NPQ and ETR under UV-B radiation. The enhancement of NPQ in our experiment should be related to the decrease of F_0 caused by thermal dissipation enhancement within the light-harvesting antennas system, which was a defensive mechanism of plants under stress environment.

Collectively, analysis of chlorophyll fluorescence data proved that UV-B radiation negatively affected PSII

function, and exogenous JA treatment promoted almost all of the fluorescence parameters, especially with 1 mM JA. Moreover, the decrease of PSII function caused by UV-B treatment was alleviated in the presence of JA, such as improved maximal photochemical efficiency, reaction centers excitation energy capture efficiency, effective PSII quantum yield, and photosynthetic electron transport rate.

Conclusion

In summary, the present study confirmed that JA counteracted in part the negative effects of UV-B radiation. JA-induced strategies of UV-B tolerance in wheat seedlings mainly included accumulation of anthocyanin and osmotic adjustment substances, enhanced activity of SOD enzymes, and improved PSII function by increasing F_v/F_m, ΦPSII, and ETR and enhancing the NPQ process under UV-B stress.

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