Field Crops Research 171 (2015) 79–85

Contents lists available at ScienceDirect

Field Crops Research

journal homepage: www.elsevier.com/locate/fcr

# Ambient UV-B radiation inhibits the growth and physiology of *Brassica napus* L. on the Qinghai-Tibetan plateau

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ARTICLE INFO

*Article history:*
Received 12 October 2014
Received in revised form
11 November 2014
Accepted 16 November 2014
Available online 2 December 2014

*Keywords:*
*Brassica napus* L.
Plant growth
Qinghai-Tibetan plateau
UV-B radiation

ABSTRACT

Increased amounts of ultraviolet-B (UV-B) radiation reaching the Earth's surface through stratospheric ozone depletion are expected to have a negative effect on plant responses. However, the reliability of extrapolating indoor experiments to infer plant responses under field conditions has been questioned. Here, we report the growth and physiological responses of *Brassica napus* L. crops grown on the Qinghai-Tibetan plateau to different levels of ambient UV-B radiation (100%, 70%, and 25%). Here, we aimed to obtain a realistic evaluation of the effect of high UV-B radiation on *B. napus* L. crops in this region. We used three experimental groups: control (ambient UV-B radiation), T1 (25% exclusion of solar UV-B), and T2 (70% exclusion of solar UV-B). Compared to the control, exclusion of solar UV-B radiation enhanced specific leaf weight (SLW) and caused plant height increased with a significant increase in biomass. Ambient UV-B radiation caused the UV-B absorbing compounds of the leaves to increase, while chlorophyll a, b, and (a + b) content decreased. No significant differences in carotenoid content were detected among the three groups. Compared to the control, exclusion of solar UV-B radiation reduced antioxidant enzyme activity. Moreover, the results showed that exposure to UV-B radiation caused *B. napus* to (i) increase UV-B absorbing compounds to reduce the transmittance of UV photons through the leaf tissue, (ii) enhance antioxidant enzyme activity to scavenge reactive oxygen species (ROS), and (iii) increase carotenoids to prevent oxidative damage. However, the bleaching of chlorophyll a and damage to the photosynthetic apparatus by solar UV-B radiation caused a reduction in the photosynthetic rate.


## 1. Introduction

Solar ultraviolet radiation is a fraction of the solar electromagnetic spectrum that is generally divided into three classes: UV-A (320–400 nm), UV-B (280–320 nm), and UV-C (≤280 nm). The level of UV-A reaching the Earth's surface is independent of ozone concentration, because it is not attenuated by ozone, and it causes negligible damage to biological systems (Caldwell and Flint, 1997; Solomon, 2008). In contrast, UV-C is highly energetic and extremely damaging to biological systems (Staehelin et al., 2001). Yet, ozone and oxygen in the stratosphere can strongly absorb UV-C and remove from sunlight reaching the Earth's surface (de Gruijl and van der Leun, 2000). The level of UV-B radiation reaching the Earth's surface is mainly influenced by the stratospheric ozone, which is the primary UV-B absorbing component in the atmosphere. Ninety percent of UV-B is directly absorbed by the ozone (Staehelin et al., 2001; McKenzie et al., 2007).

The depletion of stratospheric ozone results from the emission of human-made chemicals (e.g., chlorine and bromine compounds), leading to enhanced levels of solar UV-B irradiation reaching the Earth's surface (de Gruijl and van der Leun, 2000; Rowland, 2006). Since the 1970s, there has been great concern about ozone depletion and its consequences on the biosphere, because lower ozone concentrations lead to increased exposure to harmful solar UV-B (Madronich et al., 1998). Although UV-B only represents a fraction of the solar spectrum, it may exert substantial photobiological effects when absorbed by important macromolecules, such as proteins and nucleic acids (Ries et al., 2000; Watanabe et al., 2006). The increment of UV-B may affect terrestrial vegetation and ecosystems, causing a harmful effect on plant growth (Mackerness, 2000; Mpoloka, 2008). Numerous studies have demonstrated that the negative effects of increased UV-B are associated with a reduction in net photosynthesis, damage to photosystem II (PS II), and a

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http://dx.doi.org/10.1016/j.fcr.2014.11.006
0378-4290/

decrease in chlorophyll concentrations, among other effects (Xiong, 2001; Albert et al., 2008). However, most of these studies were conducted in growth chambers and greenhouses under conditions that did not reflect the natural environment, in addition to using controls that elevated UV-B and with low background UV-A and visible light (Xu and Sullivan, 2010). Therefore, differences noted among studies might be attributed to the experimental conditions of these evaluations, as both growth chambers and greenhouse experiments were conducted, which might lead to different responses (Searles et al., 2001). Consequently, the degree of harm that UV-B causes to plant growth remains under discussion. Of concern, important changes in future crop production could be associated with plant growth and development under increased UV-B irradiation, particularly if crop plants are sensitive to enhanced UV-B irradiation (Hakala et al., 2002; Gao et al., 2003; Hidema and Kumagai, 2006). To obtain an accurate evaluation of how UV-B will affect crop plants, the experiments of the current study were conducted under field conditions.

Researchers that contributed to the World Climate Research Programme's project on stratospheric processes suggested that maximal ozone and peak UV-B levels will occur over the next decade, with a return to pre-1980 levels of stratospheric ozone and UV-B by the middle of this century (Andrady et al., 2009, 2010). However, the same researchers warn that the complicating effect of greenhouse gases might also lengthen the process. Recent evidence indicated that there is also a significant upward trend in solar UV-B irradiation at middle and high latitudes in the northern hemisphere (Schrope, 2000; Andrady et al., 2010). This phenomenon is particularly important for the Qinghai-Tibetan plateau, which is known as the "Roof of the World," and, as such, is the most sensitive region to the global climate change (Wang et al., 2006; Shimono et al., 2010). The mean daily UV-B doses in this region are higher than those of other areas at similar latitudes. Bian (2009) showed that the amount of ozone over the Qinghai-Tibetan plateau has noticeably decreased in the last few decades. Consequently, the plants that grow on the Tibetan plateau are exposed to an environment with higher solar UV-B radiation than the surrounding regions.

Our research group has previously evaluated physiological and photosynthetic responses of various alpine plants (including *Gentiana straminea*, *Microula sikkimensis*, and *Saussurea nigrescens*) under supplemented UV-B radiation field conditions in the Qinghai-Tibetan plateau (Shi et al., 2004). Although the negative effect of elevated UV-B on alpine plants has already been reported (Day and Neale, 2002; Lutz et al., 2005), the adverse effect of ambient UV-B on crop plants and agricultural systems in the Qinghai-Tibetan plateau has received limited attention. Yet, *Brassica napus* is the most extensively grown oil crop on the plateau. Thus, the future productivity of this area could be challenged by both (i) the anticipated increase in UV-B levels and (ii) the sensitivity of *B. napus* to higher UV-B radiation.

Here, we designed a field experiment to obtain a realistic evaluation of the effects of ambient UV radiation on *B. napus* crops grown under the climatic conditions of the Qinghai-Tibetan plateau. Plant responses were analyzed in terms of morphological and physiological parameters.

## 2. Materials and methods

### 2.1. Experimental site, plant material, and treatments

A field experiment was conducted at the Nursery Experimental Centre (altitude 2300 m), which is run by the Northwest Institute of Plateau Biology, Chinese Academy of Sciences, China. The center is located in the northeast part of the Tibetan plateau, and is characterized by a typical plateau continental climate that is dominated by the southeast monsoon from May to September in summer and high pressure from Siberia in winter. Summers are short and cool, while winters are long and severely cold. The mean annual temperature is 6.1 °C and mean annual precipitation is 371.2 mm, of which over 80% falls during the summer monsoon season.

Seeds of a *B. napus* cultivar (Qingza 303) were used. This cultivar is suitable for growth at altitudes below 2800 m, at which there is a short frost-free period. Seeds of uniform size and shape were selected, washed with distilled water, and sown in plots. Each treatment plot was 1.5 m × 0.8 m with three replicates of three treatments. Four border-protective rows were placed around each plot to reduce marginal effects. The substrate used for growing the seedlings was sieved topsoil from an alpine meadow. Seeds were planted in plots under UV cut off films and were exposed to natural sunlight. The UV film was wrapped around aluminum frames (1.5 × 0.8 × 0.75 height) under which the plots were maintained. The treatments included two UV-B exclusion treatments, designated as T1 (25%) and T2 (70%), and a control, designated as CK (100%). The transmission characteristics of the plastic films did not change during the experimental period. In addition, the plastic films did not emit fluorescence in the visible region. The frames received full solar radiation for most of the day without any shading, and the height of the frames was adjustable. For T1, the aluminum frames were wrapped with 0.75 mm thick cellulose diacetate (C.A.) film that reduced solar UV-B transmission by 25%. For T2, sunlight was filtered through 0.13 mm thick polyester plastic film cut off filters (Luminar, Toray Co., Tokyo, Japan), which specifically eliminate 70% solar UV-B radiation. The control (without any film wrapped around the frames) plants were grown under natural conditions. The UV-B irradiation that reached the top of the plants was measured by an ultraviolet radiation meter (Macam UV203, UK), and was checked every two days, with the height of the frames being adjusted as plants grew. The films were changed once a week to ensure uniformity in UV-B transmission.

### 2.2. Morphological features

After 45 days of treatment (during the early reproductive stage, when the inflorescence is visible at center of the rosette), 15 plants from each replicate were harvested and the morphological parameters were analyzed (plant height, leaf area, biomass, and specific leaf weight [SLW]). Biomass was obtained after oven drying at 80 °C for 48 h. Leaf area was determined with a portable leaf area meter (LI-COR, LI-3000, Lincoln, Nebraska, USA).

### 2.3. Photosynthetic pigments and UV-B absorbing compounds

Fully expanded and mature leaves were collected at the green bud stage from each frame of all replicates. Then, 45 leaf discs of 7 mm diameter were punched from the leaf blade of the leaves from the replicates of all three treatments. Then, the leaf discs were randomly divided into three groups, and were placed in bottles containing 10 ml extracting solution ($V_{ethanol} : V_{acetone} : V_{H_2O} = 45 : 45 : 1$), and were then kept in a cool and dark place for 2 weeks. The absorbance of the extracted solutions was read at 647 and 664 nm with a UV-spectrophotometer (UV-1750, Shimazu, Japan). The photosynthetic pigments were determined as described by Qaderi and Reid (2005). Another set of 45 leaf discs (also 7 mm diameter) from leaves at the green bud stage were used to extract UV-absorbing compounds in acidified methanol ($V_{methanol} : V_{H_2O} : V_{HCl} = 79 : 20 : 1$), which were also kept in a cool and dark place for 2 weeks. UV-B absorbing compounds were estimated by measuring absorbance from 250 to 400 nm with a UV-spectrophotometer (UV-1750, Shimazu, Japan). Photosynthetic pigments were estimated by

measuring absorbance at 663, 645, and 440 nm. Each experiment was repeated six times (Shi et al., 2004; Treutter, 2005).

### 2.4. Antioxidant enzymes activity and malondialdehyde (MDA) content

To determine antioxidant enzyme activity, extracts were prepared from 1.0 g of fully developed leaves homogenized under ice-cold conditions in 5 ml of extraction buffer, containing 50 mM phosphate buffer (pH 7.4), 1 mM ethylene diaminetetraacetic acid (EDTA), 1 g polyvinylpyrrolidone (PVP), and 0.5% (v/v) Triton X-100. The homogenates were centrifuged at 10,000 × *g* for 30 min, and the supernatant fraction was used for the assays.

Superoxide dismutase activity (SOD) was assayed by the inhibition of the photochemical reduction of nitroblue tetrazolium (NBT), as described by (Costa et al., 2002). The reaction mixture consisted of 50 μl enzyme extract and 3.0 ml $O_2^-$ generating mixture solution, containing 50 mM potassium-phosphate (pH 7.8), 0.1 mM $Na_2$-EDT, 13 mM methionine, 75 μM NBT, and 16.7 μM riboflavin. The test tubes were shaken and placed 30 cm from a light bank consisting of six 15-W fluorescent lamps. The reaction was allowed to run for 10 min, and was stopped by switching off the light. The reduction in NBT was followed by reading the absorbance at 560 nm. The blanks and controls were run the same way, but without illumination or enzymes, respectively. One unit of SOD was defined as the amount of enzyme that caused 50% inhibition of NBT reduction under the assay conditions (Costa et al., 2002).

Catalase activity (CAT) was determined in the homogenates by measuring the decrease in absorption at 240 nm in a reaction medium containing 50 mM potassium phosphate buffer (pH 7.2), 10 mM $H_2O_2$, and 50 μl enzyme extract. The activity was calculated using the extinction coefficient (40 $mM^{-1}$ $cm^{-1}$) for $H_2O_2$.

Peroxidase activity (POD) was based on determining guaiacol oxidation (extinction coefficient 26.6 $mM^{-1}$ $cm^{-1}$) at 470 nm by $H_2O_2$. The reaction mixture contained 50 mM potassium phosphate buffer (pH 7.0), 20.1 mM guaiacol, 12.3 mM $H_2O_2$, and enzyme extract in a 3 ml mixture volume (Gao and Zhang, 2008).

MDA content was determined by the thiobarbituric acid (TBA) reaction. The homogenate was centrifuged at 3500 g for 20 min. To 2 ml of the aliquot of the supernatant, 2 ml of 20% TCA containing 0.5% (w/v) TBA and 100 ml of 4% (w/v) butylated hydroxytoluene in ethanol were added. The mixture was heated at 95 °C for 30 min, and was then quickly cooled on ice. The contents were centrifuged at 10,000 × *g* for 15 min, and the absorbance was measured at 532 nm (He and Hader, 2002).

### 2.5. Chlorophyll fluorescence

Chl fluorescence parameters were recorded in the field with a portable fluorescence induction monitor (FMS-2, Hansatech, UK). Measurements were made on the mature fully expanded leaves (usually the third or fourth leaf from the apex) after a 20 min dark adaptation period between 10:00 and 11:00 (local solar time). Dark adaptation time was the time needed to obtain a steady value of *Fv*/*Fm* (Maximum quantum efficiency of PSII photochemistry) (Baker and Oxborough, 2004). Leaf clips were applied to the leaflets of 15 plants that were fully exposed to the sun, which were randomly sampled in the center of each plot.

### 2.6. Data analysis

The experimental design was a randomized complete block with three groups, and each treatment was replicated three times. All data are presented as means of the 15 samples. The difference between the means was tested with the independent-samples *t*-test ($p < 0.05$). Data analyses were performed by SPSS (version 16.0), and the results were expressed as mean ± S.E. (standard error).

## 3. Results

### 3.1. Plant height, SLW, and biomass

After 45 days, the *B. napus* plants from the three treatments showed noticeable changes in plant height, SLW, and biomass (Fig. 1). The UV-B constituents present in the solar spectrum seemed to inhibit the photo-morphogenetic pattern. Compared to the control, plant height was enhanced by about 1.06 cm and 2.27 cm in the T1 and T2 UV-B exclusion treatments, respectively (Fig. 1a). Although no significant differences were detected in SLW among the three plant treatments, SLW increased with reduced UV-B exposure (Fig. 1b). Compared to the control, UV-B exclusion plants exhibited a significant increase in biomass (Fig. 1c), the plant biomass of T1 and T2 increased by about 12% and 20%, respectively.

### 3.2. Photosynthetic pigments and UV-B absorbing compounds

Compared to the control, the Chl-a and Chl-b content per unit area of leaf increased with ambient solar UV-B radiation attenuation, with this result being statistically significant except for plants with 25% UV-B exclusion (Table 1). The opposite trend was recorded for carotenoid content, but there was no significant decrease among the three treatments (Table 1).

Plants are constantly subjected to environmental stress during their whole life time; however, plants are able to activate defense systems in response to stress. Many plants are able to adapt to high UV-B radiation by producing secondary metabolites, which absorb UV-B radiation. The accumulation of UV-B absorbing compounds in the leaves was the most apparent effect of ambient UV-B radiation (control) when compared to 70% UV-B exclusion (Table 1).

### 3.3. Antioxidant enzymes activity and MDA content

Ambient UV-B radiation changed the activity of antioxidant enzymes. SOD, and CAT activity significantly decreased with ambient solar UV-B radiation attenuation, whereas POD activity increased by UV-B exclusion (Fig. 2a–c). Fig. 2d shows that UV-B radiation causes the enhancement of membrane peroxidation in leaf tissues, which, in turn, increases leaf MDA content. Compared to the control, leaf MDA content was significantly lower in UV-B exclusion plants.

### 3.4. Chlorophyll fluorescence parameters

We found that the ratio of *Fv*/*Fm* decreased significantly in CK compared with T1 and T2 plants (Table 2). In addition, there was no noticeable difference between T1 and T2 plants. We also analyzed the Kautsky transient in the leaves of *B. napus* plants, and computed various transient parameters, including PSII maximum efficiency (*Fv*′/*Fm*′), nonphotochemical quenching (*NPQ*), and photochemical quenching (*qP*). We found that the *Fv*′/*Fm*′ ratio increased with ambient UV-B radiation attenuation, with a significant increase between CK and T2 (Table 2). In contrast, the *NPQ* declined in leaves that grew under ambient UV-B radiation; however, there was no significant difference among the three experimental treatments. The experimental data indicated that the variation tendency of *qP* was similar to that of *Fv*′/*Fm*′ (Table 2).

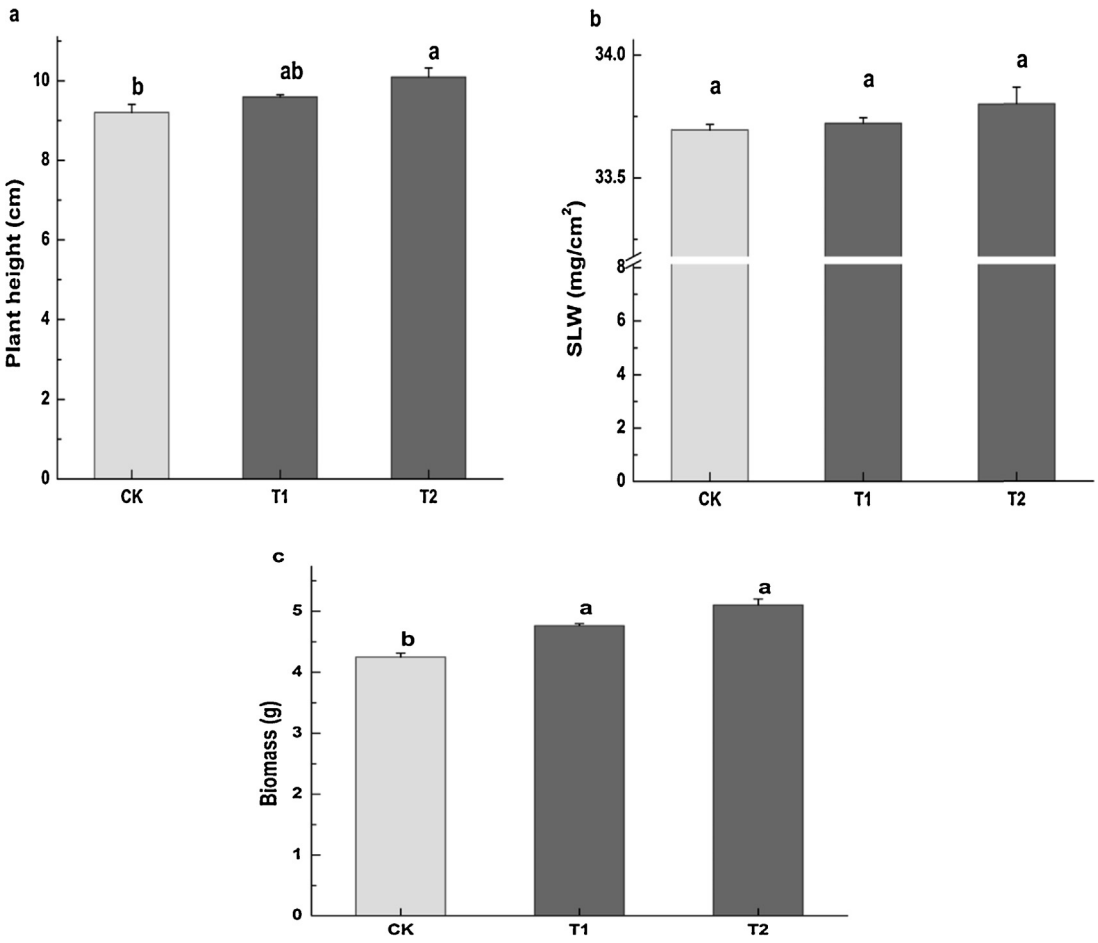


**Fig. 1.** Effect of UV-B radiation on the plant height, specific leaf weight (SLW) and biomass of *B. napus* in the Qinghai-Tibetan plateau. Different lower-case letters indicate significant differences ($p < 0.05$) according to ANOVA analysis. The vertical bar indicates the ±SE of the means. Plants raised under normal sunlight represent the control (CK); 25% exclusion of solar UV-B (T1); 70% exclusion of solar UV-B (T2); (a) the height of *B. napus* was significantly increased by 70% exclusion of solar UV-B; (b) the specific leaf weight (SLW) of *B. napus* was increased with ambient UV-B exclusion; (c) the biomass showed a significant decrease when exposing to ambient UV-B radiation.

## 4. Discussion

Stratospheric ozone depletion causes an increase in the amount of UV-B radiation that reaches the Earth's surface (Albert et al., 2008). Enhanced solar UV-B radiation might disrupt cellular homeostasis and impair plant growth and development (Amudha et al., 2005; Li et al., 2010). To tolerate UV-B stress, plants have evolved sophisticated mechanisms that involve altered physiological and biochemical processes (Tuteja et al., 2001; Caldwell et al., 2003). This study reports the growth and performance responses of

**Table 1**
Changes in photosynthetic pigment content and UV-B absorbing compound concentrations of *B. napus* leaves affected by solar UV-B radiation in the Qinghai-Tibetan plateau.

| Treatment | Photosynthetic pigments | | | | UV-B absorbing compounds (A/cm²) |
|---|---|---|---|---|---|
| | Total Chl (mg/g) | Chla (mg/g) | Chlb (mg/g) | Car (mg/g) | |
| CK | 11.008 ± 0.062b | 8.323 ± 0.063b | 2.68 ± 0.017b | 0.421 ± 0.013a | 0.318 ± 0.013a |
| T1 | 11.142 ± 0.051b | 8.449 ± 0.161b | 2.69 ± 0.015b | 0.416 ± 0.025a | 0.314 ± 0.002a |
| T2 | 11.408 ± 0.062a | 8.689 ± 0.186a | 2.72 ± 0.025a | 0.408 ± 0.016a | 0.301 ± 0.021b |

Different lower-case letters indicate significant differences ($p < 0.05$) according to ANOVA analysis. CK (ambient UV-B radiation); T1 (25% exclusion of solar UV-B); T2 (70% exclusion of solar UV-B); Chl, chlorophyll; Chla, chlorophyll a; Chlb, chlorophyll b; Car, carotenoid.

**Table 2**
Effect of solar UV-B radiation on the chlorophyll fluorescence parameters of *B. napus* leaves in the Qinghai-Tibetan plateau.

| Treatment | Parameter | | | |
|---|---|---|---|---|
| | *Fv*/*Fm* | *Fv*′/*Fm*′ | *NPQ* | *qP* |
| CK | 0.7153 ± 0.0046b | 0.6299 ± 0.0073b | 1.9802 ± 0.0341a | 0.6581 ± 0.0030b |
| T1 | 0.7337 ± 0.0021a | 0.6442 ± 0.0019ab | 1.9503 ± 0.1996a | 0.6817 ± 0.0146a |
| T2 | 0.7399 ± 0.0119a | 0.6707 ± 0.0175a | 1.9419 ± 0.0372a | 0.7006 ± 0.0564a |

Different lower-case letters indicate significant differences ($p < 0.05$) according to ANOVA analysis. CK (ambient UV-B radiation); T1 (25% exclusion of solar UV-B); T2 (70% exclusion of solar UV-B); *Fv*/*Fm*, maximum quantum efficiency of PSII photochemistry; *Fv*′/*Fm*′, PSII maximum efficiency; *NPQ*, nonphotochemical quenching; *qP*, photochemical quenching.

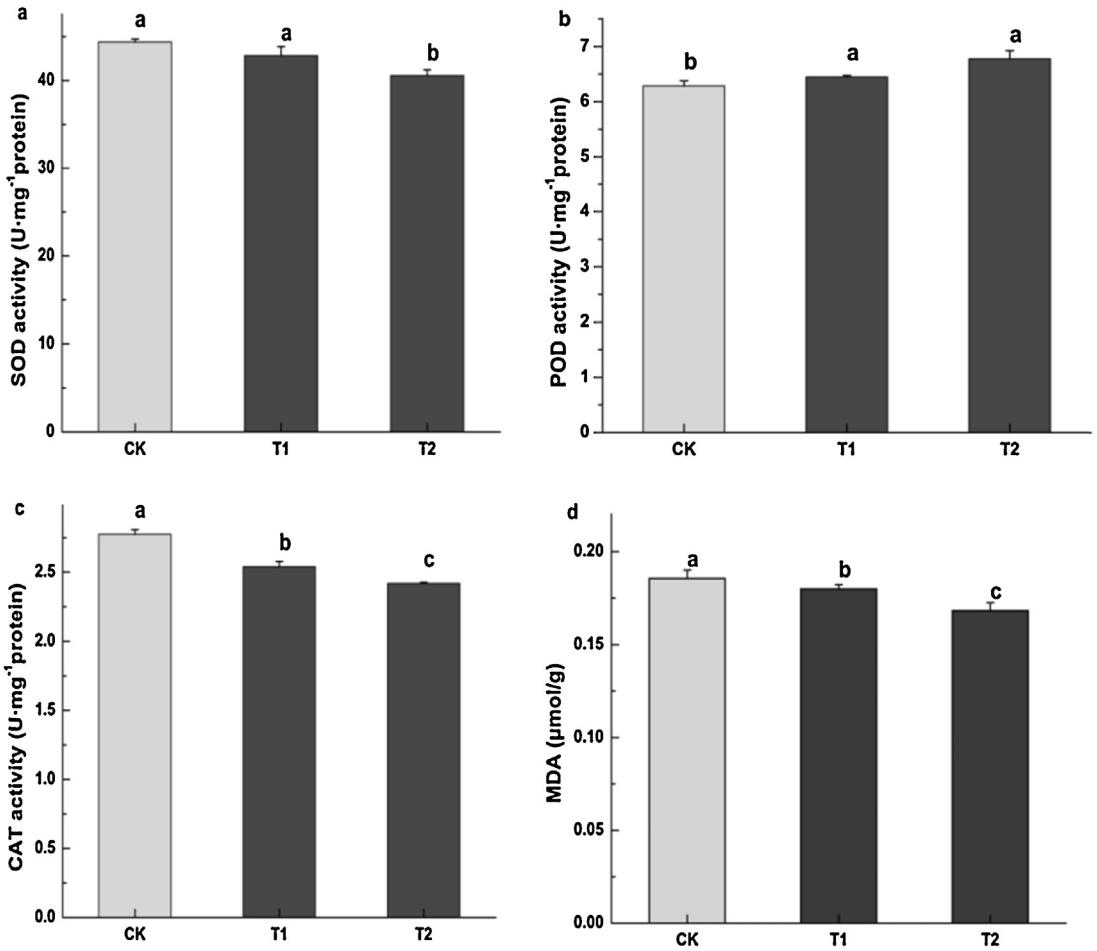


**Fig. 2.** Antioxidant enzymes activities and malondialdehyde (MDA) content of *B. napus* leaves affected by ambient UV-B radiation in the Qinghai-Tibetan plateau. Different lower-case letters indicate significant differences ($p < 0.05$) according to ANOVA analysis. The vertical bar indicates the ±SE of the means. Plants raised under normal sunlight represent the control (CK); 25% exclusion of solar UV-B (T1); 70% exclusion of solar UV-B (T2); (a) the superoxide dismutase (SOD) activity of *B. napus* leaves was significantly decreased by 70% exclusion of solar UV-B; (b) the peroxidase (POD) activity of *B. napus* leaves was significantly increased by excluded UV-B; (c) the catalase (CAT) activity of *B. napus* leaves showed an obvious decreased trend at different UV-B radiation levels; (d) the malondialdehyde (MDA) content of *B. napus* leaves affected by ambient UV-B and UV-B exclusion conditions.

*B. napus* exposed to ambient UV-B radiation on the Qinghai-Tibetan plateau under field conditions. The results are expected to help assess the actual influence of enhanced UV-B on agricultural crops due to stratospheric ozone depletion. The results indicated that UV-B radiation had a negative effect on the morphology and photosynthetic performance of *B. napus* in the Qinghai-Tibet Plateau.

Changes in plant morphological parameters are used as an index to assess the degree of UV-B radiation sensitivity (Antonelli et al., 1997; Zu et al., 2010). In this study, the analysis of morphological parameters indicated a dramatic increase in the plant height, SLW, and biomass of *B. napus* plants raised under UV-B exclusion conditions compared with control plants (i.e., grown under full solar UV-B radiation, Fig. 1). We observed a significant increase in *B. napus* plant height with solar UV-B radiation attenuation during the early reproductive stage (i.e., when the inflorescence was visible at the center of the rosette). Compared to control plants, plants raised T2 conditions were significantly taller, by about 24.6% (Fig. 1a). The effects of ambient UV-B radiation on *B. napus* SLW are shown in Fig. 1b. Plant biomass was also enhanced with ambient UV-B radiation attenuation (Fig. 1c). This result is consistent with existing studies, showing that elevated UV-B radiation causes plant height, SLW, and biomass to decrease (Li et al., 2010). Furthermore, Amudha et al. (2005) found that the removal of UV-B from natural solar radiation caused a large increase in the growth of *Cyamopsis* species.

UV-B screening compounds are of physiological importance because they help protect plants from the damage caused by UV-B radiation by reducing the transmittance of UV photons through leaf tissue (Smith et al., 2000; Treutter, 2005). In the current study, we found that after 45 days of solar UV-B radiation exclusion, the accumulation of UV-B screening compounds in *B. napus* leaves declined. This result indicates that these compounds improve epidermal UV screening (Table 1). Sullivan (2005) observed that PS II is protected against UV-B damage by epidermal screening, which is associated with an increase in leaf phenolics and flavonoids. Gao et al. (2004) also demonstrated that enhanced UV-B irradiance increases flavonoid accumulation in maize leaves. These flavonoids absorb large amounts of 280–315 UV radiation and help prevent UV-B from reaching the mesophyll and affecting photosynthesis. Yet, our results also showed that the carotenoid content was higher in *B. napus* leaves exposed to ambient UV-B radiation compared to UV-B radiation exclusion conditions. In addition, the chlorophyll content was raised in *B. napus* leaves subject to UV-B radiation exclusion (Table 1). Some studies have shown that carotenoids have a protective function against UV-B radiation (Demmig-Adams and Adams III, 1996; Matsubara et al., 2008). Carotenoids protect the photosynthetic apparatus from photooxidative damage by quenching $^3$Chl* and ROS (Fedina et al., 2003). The efficacy of carotenoids at protecting the two photosystems may be due to their function as efficient quenchers of high-energy shortwave

radiation (Bilger and Björkman, 1990; Johnson et al., 1993). Functionally, the carotenoids, especially xanthophylls, absorb the shortest wavelength radiation within the light harvesting complexes. While both UV-B absorbing compounds and carotenoids increase in response to UV-B radiation, there remains speculation as to whether it is related to the protection of photosynthesis. The results of our study indicate that increased carotenoid production and changes to the proportions of photosynthetic pigments may also contribute to the protection of plant functioning from the deleterious effects of UV-B.

Antioxidative enzymes are typically involved in the mechanisms of biochemical adaptation in living organisms subjected to stress conditions, and may function as a ROS scavengers to prevent membrane damage and protein denaturation (Yannarelli et al., 2006). Previous studies have shown that enhanced UV-B radiation produces oxidative stress and increases ROS in plants, such as superoxide radicals ($O_2^-$), singlet oxygen ($O^•$), hydrogen peroxide ($H_2O_2$), and hydroxyl radicals (OH). These compounds influence a number of metabolic functions in plants (Santos et al., 2004; Wang et al., 2010). Many of the deleterious effects of UV-B on photosynthesis could be caused by the generation of free radicals that destroy various components of the photosynthetic apparatus (Sullivan and Rozema, 1999; Albert et al., 2008). In the enzymatic defense system, SOD scavenges $O_2^-$ by transforming it into $H_2O_2$. Subsequently, the over-produced $H_2O_2$ is reduced to $H_2O$ by POD and CAT antioxidases at different cellular locations (Green and Fluhr, 1995; He and Hader, 2002). SOD, POD, and CAT enzymes are important for protecting plants against oxidative damage. The results of this study clearly show a decline in SOD activity in *B. napus* leaves with ambient UV-B radiation attenuation (Fig. 2a). This result indicates that UV-B induces SOD activity in leaves to effectively scavenge over-produced $O_2^-$. Excess $O_2^-$ may produce higher levels of $H_2O_2$ in control plants under ambient UV-B conditions. In addition, ambient UV-B radiation increased CAT activity in *B. napus* leaves (Fig. 2c). However, increased CAT activity did not enhance the POD activity (Fig. 2b) of *B. napus* leaves under ambient UV-B conditions. ROS may react with lipid membranes causing their peroxidation, which leads to membrane damage, resulting in increased concentrations of MDA-lipid peroxidation products. The degree of lipid peroxidation is often assessed by MDA content, and is often used as an indicator of physiological stress in plants (Fedina et al., 2003). Similar results were obtained in the current study (Fig. 2d).

The depletion of stratospheric ozone has led to enhanced levels of UV-B radiation in the solar spectrum and, consequently, a large proportion of UV-B reaches the Earth's surface, with serious implications for all organisms. In particular, photosynthetic organisms are inevitably exposed to higher solar UV-B radiation on the Qinghai-Tibet plateau. High levels of UV-B radiation may affect photosynthesis indirectly by the photobleaching and photodegradation of photosynthetic pigments (Teramura and Ziska, 2004). Chlorophyll fluorescence is a parameter that is often used to determine the abiotic and biotic stress effects of UV-B on photosynthetic performance (Baker, 2008). When plants are exposed to UV-B stress, chlorophyll fluorescence is frequently perturbed. This phenomenon is so widespread that the measurement of chlorophyll fluorescence parameters provides a simple and rapid way of monitoring UV-B stress (Kakani et al., 2003; Gao and Zhang, 2008). This technique was used in the current experiment to monitor the changes to chlorophyll fluorescence in response to ambient UV-B radiation in *B. napus* leaves. Compared to pants grown under UV-B exclusion, $Fv/Fm$, $Fv'/Fm'$, and $qP$ consistently declined in the control plants after 45 days. In contrast, the opposite trend was observed for NPQ. These results strongly indicate that current of UV-B radiation in the Qinghai-Tibet plateau inhibits *B. napus* photosynthetic performance. The negative effects of UV-B on photosynthetic processes have also been demonstrated in preceding studies (Teramura and Ziska, 2004; Caldwell et al., 2007).

In conclusion, current UV-B radiation levels on the Qinghai-Tibet plateau slightly inhibit the growth of *B. napus* during the early reproductive stage. In addition, current UV-B levels interfere with various physiological processes, causing membrane lipid peroxidation, chlorophyll bleaching, changes to antioxidant enzyme activity, and a decrease in photosynthetic electron transport. Although our results demonstrated that UV-B negatively affects *B. napus* growth and development on the Qinghai-Tibet plateau, the effects of UV-B on the yield and quality of this crop remain still unknown. Therefore, it is necessary to conduct experiments investigating the effect of UV-B stress on the yield and quality of *B. napus* crops on the Qinghai-Tibet plateau.

## Conflict of interest

None.

## Acknowledgements

This research was supported by the Natural Science Foundation of China (30170154). We thank Prof. Shi Sheng-Bo and Prof. Han Fa for their helpful advice on this study, and Yanxia Shang, Qinghai Liu, Jun Wen, and Yunting Lei for their help in both the field and the laboratory experiments.

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