



Photosynthesis of *Saussurea superba* and *Gentiana straminea* is not reduced after long-term enhancement of UV-B radiation

Sheng-Bo Shi^{a,*}, Wen-Yan Zhu^a, Hui-Mei Li^a, Dang-Wei Zhou^a,
Fa Han^a, Xin-Quan Zhao^a, Yan-Hong Tang^b

^a Northwest Institute of Plateau Biology, The Chinese Academy of Sciences, 59 Xi-Guan Street,
Xining, Qinghai 810001, People's Republic of China

^b National Institute for Environmental Studies, Onogawa 16-2, Tsukuba 305-0053, Japan

Received 5 November 2002; received in revised form 15 June 2003; accepted 15 June 2003

Abstract

Experiments were conducted in an alpine *Kobresia humilis* meadow near Haibei Alpine Meadow Ecosystem Research Station (37°29'–37°45'N, 101°12'–101°33'E; altitude 3200 m). Effects of enhanced ultraviolet-B (UV-B) radiation on photosynthesis of the alpine plants of *Saussurea superba* and *Gentiana straminea* were investigated. Both species were exposed to a UV-B_{BE} density at 15.80 kJ m⁻² per day, simulating nearly 14% ozone (O₃) reduction during the plant growing season. Neither photosynthetic CO₂ uptake rate nor photosynthetic O₂ evolution rate were decreased after a long period of enhanced UV-B radiation treatment. On the contrary, there was a tendency to increase of both parameters in both species. The photosynthetic pigments were also increased, when expressed on a leaf area basis. UV-B absorbing compounds, detected by the absorbance values at 300 nm, had a tendency to increase in both species after enhanced UV-B radiation. After long-term exposure of plants to enhanced UV-B radiation, leaf morphology was also affected. Leaf thickness in both *S. superba* and *G. straminea* were increased significantly ($P < 0.001$). This supports our hypothesis that the increase of leaf thickness in both species after long-term exposure of enhanced UV-B radiation could compensate for the photodestruction of photosynthetic pigments when light passes through the leaf. Therefore, photosynthesis is not reduced in either species when expressed on leaf area basis.

© 2003 Elsevier B.V. All rights reserved.

Keywords: Adaptation; Alpine plants; Leaf morphology; Ozone depletion; Qinghai-Tibet Plateau

1. Introduction

Solar ultraviolet-B (UV-B; 280–315 nm) radiation can partially penetrate the atmosphere and reach the Earth's surface. This could have biological con-

sequences. Solar UV-B radiation flux is higher at high elevation, because of less air mass and greater transparency of the alpine atmosphere to shorter wavelength radiation (Madronich et al., 1995). It has increased, especially at higher latitude due to stratospheric ozone (O₃) depletion mainly caused by emission of chlorofluorocarbons (CFCs) (Albritton and Watson, 1990). Recent evidence (Herman et al., 1996; Pyle, 1997; Caldwell et al., 2003; McKenzie

* Corresponding author. Tel.: +86-971-6153387;

fax: +86-971-6143282.

E-mail address: sbshi@mail.nwipb.ac.cn (S.-B. Shi).

et al., 2003) indicated that there is also a significant upward trend in solar UV-B radiation at middle and high latitudes in the northern hemisphere.

Numerous studies have been conducted to assess the effects of enhanced UV-B radiation on various organisms (Caldwell et al., 1995; Longstreth et al., 1995; Rozema et al., 1997, 1999). Effects of solar UV-B radiation on higher plants can be divided into two categories: damaging effects and photomorphogenetic effects. Damage or inhibition is often observed on photosynthesis, growth and so on, especially in sensitive species or under high UV-B doses (often in combination with unnaturally low photosynthetically active radiation (PAR) doses). Photomorphogenetic effects are often found in field studies on leaf weight ratio, plant height, branching, etc. (Caldwell et al., 1989, 1995; Johanson et al., 1995). Changes in morphology can result in reduction or increase of growth due to displacement of the competitive balance among species. Susceptibility of plants to solar UV-B radiation varied among species, and it also could be influenced by the growing conditions such as PAR, mineral deficiency, and water stress (Caldwell et al., 1995). These aspects will be very important for grassland and forest ecosystems under enhanced UV-B radiation.

The Qinghai-Tibet Plateau is known as the third polar region on Earth, being one of the most sensitive regions to the global environmental changes. Zhou et al. (1995) demonstrated that in the past decades, the total ozone level over China has decreased continuously. The situation on the Qinghai-Tibet Plateau could become very serious if this lower total level of ozone is maintained. When direct measurements of solar UV-B radiation intensity near the Earth's surface were conducted, the UV-B radiation intensity was higher in Qinghai-Tibet Plateau regions when compared with other lower elevation regions (Guo et al., 1994; Shi et al., 1999). The alpine plants growing in these regions were often under serious stresses such as low temperatures and strong solar radiation, they have adapted during a long evolution.

Our previous studies on photosynthesis indicated that in some species such as *Gentiana straminea* often increases after enhancement of UV-B radiation except in some species (Shi et al., 2001). Although this phenomenon has already been reported (Beyschlag

et al., 1988; Johanson et al., 1995), however, its reason is still not clear. In many field trials, one of the obvious phenomena was the changes in plant photomorphogenetic parameters, such as leaf thickness, leaf angle and canopy architecture (Rozema et al., 1997; Manetas, 1999). Increased leaf thickness under enhanced UV-B is likely to reduce UV-B damage to leaf cells. At the same time, reduced PAR levels in thicker leaves might reduce leaf photosynthesis (Rozema et al., 1997, 1999). At the Haibei Alpine Meadow Ecosystem Research Station (3200 m), both UV-B and PAR are higher than other two lower elevation regions such as Lanzhou (1800 m) and Nanjing (32 m) (Shi et al., 1999). Our hypothesis is that they may be important to effect negatively morphogenesis under enhanced UV-B and then subsequently leaf photosynthesis if the plants are not sufficiently adapted. In this study, we have carried out series of experiments to investigate this mechanism, we also propose an adaptation mechanism for certain alpine plants species to strong solar UV-B radiation growing in this region, and its possible impacts on photosynthesis and alpine meadow ecosystem under stratospheric ozone depletion.

2. Materials and methods

2.1. Plant materials and growth conditions

A field UV-B irradiation system has been established in the alpine *Kobresia humilis* (C.A. Mey.) Serg. meadow region near Haibei Alpine Meadow Ecosystem Research Station, The Chinese Academy of Sciences. The Research Station is located at the northeast of Qinghai-Tibet Plateau, and south hillside of the Leng-Long-Ling which is at the east of the Qilian Mountains, 37°29'–37°45'N, 101°12'–101°33'E; altitude 3200 m. It is situated in the inland with a typical plateau continental climate. As influenced by the higher elevation, the air temperature is very low with only cold and warm seasons. The annual average air temperature is -1.7°C , with the warmest month at 9.8°C , and the coldest month at -14.8°C . The annual precipitation is about 600 mm with nearly 80% mainly in the plants growing season from May to September. The air is thin with annual average of the barometric pressure at 691.4 hPa.

The alpine *K. humilis* meadow is one of the main vegetation types in these regions, containing various perennial grasses and forbs (depending on grazing intensity). The canopy structure of the plant community is simple, and plant height is low, so the primary productivity is small in this plant community. The predominance species is *K. humilis* with sub-predominance species of *Festuca ovina* Linn., *Stipa aliena* Keng and *Elymus nutans* Griseb., *Saussurea superba* Anth. and *G. straminea* Maxim. are perennial herbaceous broad-leaf species, and are mainly accompanied plant species in the *K. humilis* meadow (Zhao and Zhou, 1999). Both species are widely distributed in Qinghai-Tibet regions and also are adapted to different environments, such as hill grass, bush lawn, river rapids, alpine meadow, and so on.

2.2. UV-B setup and irradiation

The field experiment began in May 1999. It is based in open areas of alpine *K. humilis* meadow and concentrated on the impacts of enhanced UV-B radiation on the structure and function of plant community. Enhanced UV-B radiation was supplied from three of six metal frames (2.5 m × 1.3 m × 0.75 m high), each with six 40 W fluorescent lamps (UV-B-313, Beijing Electric and Light Source Institute, PR China). The UV-B radiation from the lamps was passed through a single sheet of cellulose diacetate film (0.13 mm; Courtauld Specialty Plastics, P.O. Box 5, Spondon, Derby DE2 7BP, UK) to cut-off ecologically irrelevant UV-C (<280 nm); a 0.13 mm thick clear Mylar film (E.I. du Pont de Nemours and Company, 1007 Market Street, Wilmington, DE 19898, USA) was used to absorb almost all radiation below 320 nm for the other three frames to serve as controls. The cellulose diacetate film was replaced weekly and the Mylar film biweekly. The irradiation started in early May when most of the species began to germinate, and run until mid-September when most of species entered the wither phase. The plant species were irradiated for 7 h each day centered around local solar noon time (about 13:15 h Beijing time) and controlled by timers providing a stepwise “square wave” increase of daily UV-B exposure. The enhanced UV-B_{BE} density was 15.80 kJ m⁻² per day. Enhanced UV-B treatment was the ambient solar UV-B in addition to UV-B radiation from fluorescent lamps. The model described

by Björn and Teramura (1993) was used to calculate the daily increase in UV-B radiation resulting from 14% ozone depletion under the clear day at the Haibei Alpine Meadow Ecosystem Research Station region.

2.3. Net photosynthesis rate measurement

Photosynthetic O₂ evolution rate was measured by oxygen electrode (SP-2, Shanghai Plant Physiology Institute, The Chinese Academy of Sciences). Five discs with diameter 7 mm were punched out from different leaves for measuring the net photosynthetic O₂ evolution rate according to the methods used by Li et al. (1982). The measurement conditions were as follows: the temperature was at 25 °C; PAR in the chamber was 1800 μmol m⁻² s⁻¹ supplied with a 150 W halogen lamp; CO₂ in solution was supplied by 25 mmol l⁻¹ NaHCO₃, which was dissolved in 50 mmol l⁻¹ pH 7.5 phosphate buffer.

Photosynthetic CO₂ uptake rate was measured directly in the field with a CI-301PS portable photosynthetic system (CID Inc., Washington, USA). The air was collected from an elevation of 2 m above ground.

2.4. UV-B absorbing compounds, chlorophyll, and carotenoid contents

Healthy and fully expanded leaves were collected from enhanced UV-B irradiation and ambient UV-B radiation frames. Ten leaf discs (7 mm diameter) from treated and control leaves, respectively, were put into bottles containing 10 ml methanol, HCl and H₂O (79:20:1, v/v/v) for determining UV-B absorbing compounds as described by Day et al. (1994). Other sets of 10 leaf discs were put into separate bottles containing 10 ml ethanol, acetone and H₂O (4.5:4.5:1, v/v/v), which was more stable when tightly closed bottles were kept in cold and dark for nearly 3 weeks (Zhu, 1990). Each experiment was repeated four times. The samples were filtrated and absorbance of supernatants measured. UV-B absorbing compounds were estimated by measuring absorbance from 250 to 400 nm with a UV-Vis spectrophotometer (UV-1601, Shimadzu). Chlorophylls and carotenoids were estimated by measuring absorbance at 663, 645 and 440 nm. Their calculations were made according to methods of Zhu (1990).

2.5. Leaf thickness, leaf length and leaf width

Healthy and fully expanded leaves of *S. superba* and *G. straminea* were measured directly from enhanced UV-B irradiation and ambient UV-B radiation frames. The leaf thickness was measured with a caliper (Guilin Measurement Factory, Guangxi, PR China), leaf length and leaf width were measured with a millimeter ruler.

2.6. Statistical analysis

The independent-samples *t*-test was used to assess the difference between ambient UV-B controls and enhanced UV-B treatment. Levels of significance in the differences of leaf thickness, leaf length, leaf width were analyzed by one-way ANOVA. All analyses were performed by SPSS (version 10.0) and the results were expressed as mean values and their standard deviations (S.D.).

3. Results

Both photosynthetic O₂ evolution rate (Fig. 1) and photosynthetic CO₂ uptake rate (Fig. 2) of *S. superba*

and *G. straminea* were increased or remained at the same level after long period of enhanced UV-B radiation treatment. *S. superba* had a significant difference ($P < 0.05$) between ambient UV-B and enhanced UV-B treatments in photosynthetic O₂ evolution rate (Fig. 1), while *G. straminea* had a significant difference ($P < 0.05$) in photosynthetic CO₂ uptake rate between ambient UV-B and enhanced UV-B treatments (Fig. 2).

The amounts of photosynthetic pigments were expressed both on leaf fresh weight (FW) and leaf area basis (Table 1). In *G. straminea*, on a unit fresh weight basis, enhanced UV-B radiation caused 21% increase in chlorophylls and 18% increase in carotenoids, while only 6.1% increase in chlorophylls and 6.3% increase in carotenoids measured on a leaf area basis. But only carotenoid contents measured on a fresh weight basis were significant ($P < 0.05$) between the two radiation treatments (Table 1). In *S. superba*, chlorophylls and carotenoids were slightly affected by enhanced UV-B radiation.

As an estimate of UV-B absorbing compounds, absorbance values at 300 nm were representatively chosen and expressed in A_{300} cm² (leaf area). In *S. superba*, the UV-B absorbing compounds were 2.652 ± 0.049 and 2.730 ± 0.058 in ambient UV-B

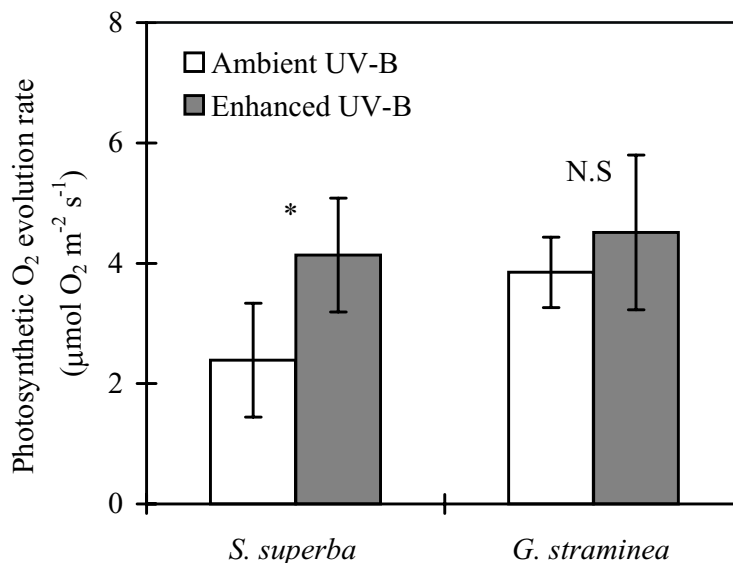


Fig. 1. Effects of enhanced UV-B radiation on photosynthetic O₂ evolution rate of *S. superba* and *G. straminea* in *K. humilis* meadow. Values are means \pm S.D. ($n = 5$). There was a significant difference between ambient UV-B and enhanced UV-B treatments only appeared in *S. superba* ($P < 0.05$). (*) Significantly different at $P < 0.05$ level with *t*-test; (N.S.) No significant difference at $P < 0.05$ level with *t*-test.

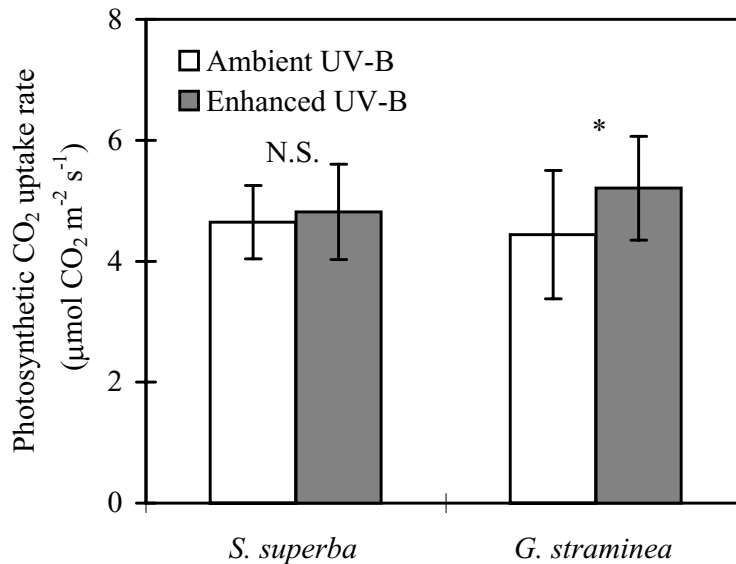


Fig. 2. Effects of enhanced UV-B radiation on photosynthetic CO₂ uptake rate of *S. superba* and *G. straminea* in *K. humilis* meadow. Values are means \pm S.D. ($n = 10$). There was a significant difference between ambient UV-B and enhanced UV-B treatments only appeared in *G. straminea* ($P < 0.05$). (*) Significantly different at $P < 0.05$ level with t -test; (N.S.), no significant difference at $P < 0.05$ level with t -test.

and enhanced UV-B treatments, respectively, in *G. straminea*, 2.087 ± 0.095 and 2.265 ± 0.146 , respectively (data not shown in figure or table). Although no significant differences in UV absorbance were detected, enhanced UV-B radiation treatment tended to increase the amount of these UV-B-absorbing compounds in both species on a leaf area basis.

After long-term enhanced UV-B radiation treatment, leaf thickness (Fig. 3) in *S. superba* and *G. straminea* increased significantly ($F = 31.012$, d.f. =

1, 158; $P < 0.001$ in *S. superba*; and $F = 32.280$, d.f. = 1, 158; $P < 0.001$ in *G. straminea*). Table 2 showed that in both species there was a decreased tendency of leaf length after enhancement of UV-B radiation, however, only *S. superba* appeared to have a significant difference ($F = 7.065$, d.f. = 1, 78; $P = 0.011$), in *G. straminea* there was no significant difference ($F = 2.669$, d.f. = 1, 78; $P = 0.106$). Enhanced UV-B treatment tended to increase leaf width ($F = 0.605$, d.f. = 1, 78; $P = 0.439$ in *S. superba*; $F = 8.053$, d.f. = 1, 78; $P = 0.006$ in *G.*

Table 1

Effects of enhanced solar UV-B radiation on chlorophyll and carotenoid concentrations in *S. superba* and *G. straminea*

Parameters	<i>S. superba</i>		<i>G. straminea</i>	
	Ambient UV-B	Enhanced UV-B	Ambient UV-B	Enhanced UV-B
Chlorophylls				
Leaf area ($\mu\text{g cm}^{-1}$)	27.90 ± 4.05	29.04 ± 3.63	26.74 ± 3.57	28.37 ± 3.16
(FW (mg g^{-1}))	1.29 ± 0.10	1.25 ± 0.11	0.98 ± 0.09	1.19 ± 0.15
Carotenoids				
Leaf area ($\mu\text{g cm}^{-1}$)	7.46 ± 0.81	7.93 ± 0.60	8.85 ± 0.58	9.41 ± 0.53
(FW (mg g^{-1}))	0.35 ± 0.02	0.34 ± 0.03	$0.33 \pm 0.01^*$	$0.39 \pm 0.02^*$

Values are means \pm S.D. ($n = 4$).

* Significantly different at $P < 0.05$.

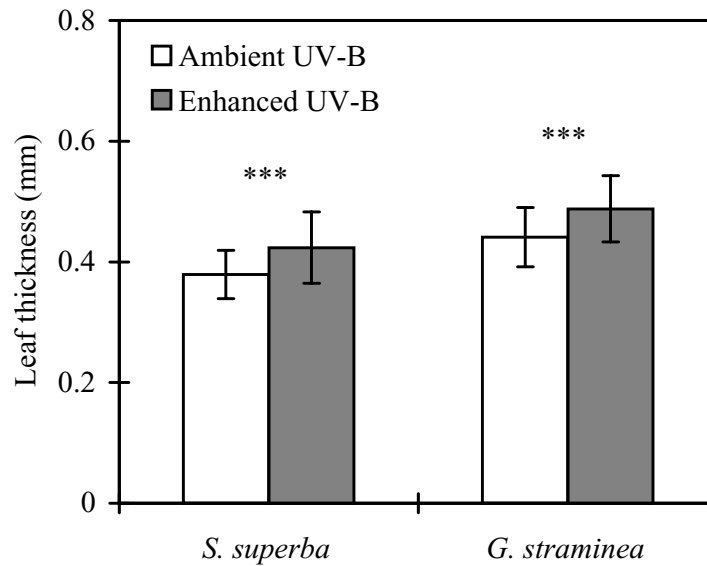


Fig. 3. Effects of enhanced UV-B radiation on leaf thickness of *S. superba* and *G. straminea*. Values are means \pm S.D. There were extremely significant differences between ambient UV-B and enhanced UV-B treatments in both species (d.f. = 1, 158; $P < 0.001$). (***) Significantly different at $P < 0.001$ level with one-way ANOVA analysis.

Table 2

Effects of enhanced UV-B radiation on leaf length and width of *S. superba* and *G. straminea*.

Treatment	<i>S. superba</i>		<i>G. straminea</i>	
	Length (cm)	Width (cm)	Length (cm)	Width (cm)
Ambient UV-B	6.92 \pm 1.27*	2.36 \pm 0.48	12.31 \pm 1.66	2.16 \pm 0.30
Enhanced UV-B	6.25 \pm 0.97*	2.45 \pm 0.53	11.70 \pm 1.64	2.40 \pm 0.44**

Values are means \pm S.D. ($n = 40$).

* Significantly different at $P < 0.05$.

** Significantly different at $P < 0.01$.

straminea), but a significant difference only appeared in *G. straminea* ($P < 0.01$).

4. Discussion

It has been reported that photosynthesis and photosynthetic productivity of some higher plants are vulnerable to increased UV-B radiation due to stratospheric ozone (O_3) depletion (Caldwell et al., 1989, 1995; Tevini and Teramura, 1989; Jordan, 1996). The damage to photosynthetic apparatus may include many aspects such as PSII reaction center, electron transfer, stomatal conductance, loss of soluble Calvin cycle

enzymes and so on (Baker et al., 1997). However, data from about three decades of studies and publications indicated that only about one-third of plant species appears to show deleterious effects on some growth responses by UV-B radiation levels above ambient, but many species exhibit no such effects (Sullivan et al., 1992; Tosserams and Rozema, 1995). This suggests that some species are already well adapted to solar UV-B radiation (Antonelli et al., 1998). In most cases, the direct UV-B-induced inhibition of photosynthetic competence was observed only at high UV-B irradiances, which were often conducted in laboratories or greenhouses (Allen et al., 1998). In the field conditions, even under extreme UV-B exposures,

acclimatization (e.g. induction of UV-B absorbing compounds) can protect the photosynthetic processes. Then some species are sensitive to current ambient levels of UV-B radiation, while others are apparently unaffected by large UV-B enhancements (Figs. 1 and 2).

On the Qinghai-Tibet Plateau, although the native plant species have already well adapted to long periods of alpine severe environmental conditions, there are also different responses to enhancement of UV-B radiation among species. In this study, no deleterious effects of enhanced UV-B radiation on photosynthesis on an area basis were detected in either alpine species measured (Figs. 1 and 2). The different photosynthetic responses in dicotyledon species, and grass and sedge species to enhanced solar UV-B radiation were detected in our trials. Dicotyledon species of *Trigonella ruthenica* had a significant difference ($P < 0.01$) with 21% decrease of photosynthetic O₂ evolution rate after enhanced UV-B treatment, but enhanced UV-B radiation did not influence the photosynthetic O₂ evolution rate in grass species of *E. nutans* and sedge of *K. humilis* (Shi, unpublished data). It appears that this species-specific responses of photosynthesis may result from consequences of physiological and morphological alterations.

Enhanced UV-B radiation changes the morphological characteristics of two species, particularly by increasing the leaf thickness (Fig. 3). This phenomenon was also reported in other studies (Chen and Bornman, 1990; Antonelli et al., 1998), but contrary to the reports on other species (Correia et al., 1999). The increase in leaf thickness could play an important role in protecting deleterious effects of UV-B radiation, and these were often accompanied by the increase in UV-B absorbing compounds in the adaxial epidermis of leaves (Antonelli et al., 1998). In this study, it is clearly demonstrated that the thicker leaves of *S. superba* and *G. straminea* by enhanced UV-B treatment may partly compensate for the photodestruction of photosynthetic pigments when light passes through the leaf, and therefore, photosynthesis is not reduced when measured on leaf area basis (Figs. 1 and 2; Table 1).

Because of structural characteristics of leaflets and its growing state near the ground, it is impossible to measure the leaf thickness directly of other species in the field, thus we are not able to make a general conclusion about their changes in leaf thickness and its relationship with photosynthesis. Of course, one

should not attribute all photosynthesis characters to the variations in leaf thickness. The higher concentrations of UV-B absorbing compounds were also contributed to the adaptation of alpine plants. These characters, maybe including DNA repair pathway and elimination capacity for active oxygen, may contribute to the protection of photosynthesis of leaves exposed to high levels of UV-B during sunny days.

In plants exposed to enhanced UV-B radiation throughout their development, a reduction in photosynthetic productivity is usually associated with a reduced ability to intercept light (i.e. smaller leaf area), and not due to an inhibition in photosynthetic competence (Allen et al., 1998). Many studies have reported that enhanced levels of UV-B can alter the balance of ecosystems both at the biochemical and whole plant levels, the balance of competition between different species may be altered during the course of their development (Gold and Caldwell, 1983; Tevini and Teramura, 1989). In this study, there were increases in leaf thickness and leaf width in both *S. superba* and *G. straminea* after enhancement of UV-B radiation (Table 2; Fig. 3). However, studies on other species such as *T. ruthenica* and *E. nutans* had opposite phenomenon (Shi, unpublished data). Different photomorphological and structural responses among species caused by long-term irradiation of UV-B may directly influence the competitive balance for light and nutrients. The changes of leaf thickness and leaf width and leaf length in *S. superba* and *G. straminea* imply a possible role for enhanced UV-B radiation, although it still needs to determine its effects on plant community and ecosystem levels. As emphasized by many researchers continued attention should be paid to accumulated effects of enhanced UV-B radiation at ecosystem level (Johanson et al., 1995; Searles et al., 2002).

More and more recent studies indicated that direct UV-B induced inhibition of photosynthesis only appeared at higher UV-B radiation levels (Keiller and Holmes, 2001; Bassman et al., 2002). However, even exposed to very high UV-B irradiation, photosynthetic process could be protected by acclimation (e.g. induction of UV-B absorbing flavonoids). Although our experiments did not show a significant difference of UV-B absorbing compounds between ambient and enhanced UV-B radiation, there was a trend to increase the amount of UV-B-absorbing

compounds in both species on a leaf area basis. Except for protection of UV-B radiation induced injury, UV-B absorbing compounds and other compounds of secondary metabolism could restrain insects and other herbivores (Zavala et al., 2001; Warren et al., 2002), and also affect pathogen infection (Kiesecker et al., 2001). Therefore, solar UV-B radiation is not just a potential environmental stress for plants, but also affects ecological processes. The influence of enhanced UV-B radiation on food chains should be considered in natural ecosystem especially in evaluating its impacts on different trophic levels.

Many studies have reported that the influence of enhanced solar UV-B radiation on natural ecosystems may include many aspects (Johanson et al., 1995; Caldwell et al., 1998; Rozema et al., 2002). Considering the global environmental changes, solar UV-B radiation interacts with other environmental factors, and thus it impacts on plants and ecosystem may be subtler. So for the evaluation of the influence of solar UV-B radiation on alpine ecosystem in Qinghai-Tibet Plateau, there is still much work to be done.

Acknowledgements

This work was financially supported by the Key Innovation Plan of the Chinese Academy of Science (KSCX2-SW-106; KSC) (2-1-07), the National Natural Science Foundation of China (30170154), and the State Key Basic Research Foundation of China (G198040813). Thanks are expressed to Prof. Lars Olof Björn, Lund University, Sweden, who provided the cellulose diacetate film and Mylar film; and to Prof. Lars Olof Björn and Dr. Andrew I. Hsiao for their critical comments and for their help in editing of this manuscript.

References

- Albritton, D.L., Watson, R.T., 1990. Scientific assessment of stratospheric ozone change: 1989. Global Ozone Research and Monitoring Project Report No. 20, WMO, Geneva.
- Allen, D.J., Nogués, S., Baker, N.R., 1998. Ozone depletion and increased UV-B radiation: is there a real threat to photosynthesis? *J. Exp. Bot.* 49, 1775–1788.
- Antonelli, F., Bussotti, F., Grifoni, D., Grossoni, P., Mori, B., Tani, C., Zipoli, G., 1998. Oak (*Quercus robur* L.) seedlings responses to a realistic increase in UV-B radiation under open space condition. *Chemosphere* 36, 841–845.
- Baker, N.R., Nogués, S., Allen, D.J., 1997. Photosynthesis and photoinhibition. In: Lumsden, P.J. (Ed.), *Plants and UV-B: Responses to Environmental Change*. Society for Experimental Biology, Seminar Series, vol. 64. Cambridge University Press, Cambridge, pp. 95–111.
- Bassman, J.H., Edwards, G.E., Robberecht, R., 2002. Long-term exposure to enhanced UV-B radiation is not detrimental to growth and photosynthesis in Douglas-fir. *New Phytol.* 154, 107–120.
- Beyschlag, W., Barends, P.W., Flint, S.D., Caldwell, M.M., 1988. Enhanced UV-B irradiation has no effect on photosynthetic characteristics of wheat (*Triticum aestivum* L.) and wild oat (*Avena fatua* L.) under greenhouse and field conditions. *Photosynthetica* 22, 516–525.
- Björn, L.O., Teramura, A.H., 1993. Simulation of daylight ultraviolet radiation and effects of ozone depletion. In: Young, A.R., Björn, L.O., Moan, J., Nultsch, W. (Eds.), *Environmental UV Photobiology*. Plenum Press, New York, pp. 41–71.
- Caldwell, M.M., Teramura, A.H., Tevini, M., 1989. The changing solar ultraviolet climate and the ecological consequences for higher plants. *Trends Ecol. E* 4, 363–367.
- Caldwell, M.M., Teramura, A.H., Tevini, M., Bornman, J.F., Björn, L.O., Kulandaivelu, G., 1995. Effects of increased solar UV radiation on terrestrial plants. *Ambio* 24, 166–173.
- Caldwell, M.M., Björn, L.O., Bornman, J.F., Flint, S.D., Kulandaivelu, G., Teramura, A.H., Tevini, M., 1998. Effects of increased solar ultraviolet radiation on terrestrial ecosystems. *J. Photochem. Photobiol. B: Biol.* 46, 40–52.
- Caldwell, M.M., Ballaré, C.L., Bornman, J.F., Flint, S.D., Björn, L.O., Teramura, A.H., Tevini, M., 2003. Terrestrial ecosystems, increased solar ultraviolet radiation and interactions with other climatic change factors. *Photochem. Photobiol. Sci.* 2, 29–38.
- Chen, Y.P., Bornman, J.F., 1990. The response of bean plants to UV-B radiation under different irradiances of background visible light. *J. Exp. Bot.* 41, 1489–1495.
- Correia, C.M., Torres-Pereira, M.S., Torres-Pereira, J.M.G., 1999. Growth, photosynthesis and UV-B absorbing compounds of Portuguese Barbel wheat exposed to ultraviolet-B radiation. *Environ. Pollut.* 104, 383–388.
- Day, T.A., Howells, B.W., Rice, W.J., 1994. Ultraviolet absorption and epidermal-transmittance spectra in foliage. *Phys. Plant* 92, 207–218.
- Gold, W.G., Caldwell, M.M., 1983. The effects of ultraviolet-B radiation on plant competition in terrestrial ecosystems. *Phys. Plant* 58, 435–444.
- Guo, S., Zhou, X.J., Zhang, X.C., 1994. Preliminary analysis of atmospheric ozone contents and ultraviolet-B radiation in Qing-Zang Plateau regions. *Chin. Sci. Bull.* 39, 50–53 (in Chinese).
- Herman, J.R., Barthia, P.K., Ziemke, J., Ahmad, Z., Larko, D., 1996. UV-B increases (1979–1992) from decreases in total ozone. *Geophys. Res. Lett.* 23, 2117–2120.
- Johanson, U., Gehrke, C., Björn, L.O., Callaghan, T.V., Sonesson, M., 1995. The effects of enhanced UV-B radiation on a subarctic heath ecosystem. *Ambio* 24, 106–111.

- Jordan, B.R., 1996. The effects of ultraviolet-B radiation on plants: a molecular perspective. In: Callow, J.A. (Ed.), *Advances in Botanical Research Incorporating Advances in Plants Pathology*, vol. 22. Academic Press, UK, pp. 97–162.
- Keiller, D.R., Holmes, M.G., 2001. Effects of long-term exposure to elevated UV-B radiation on the photosynthetic performance of five broad-leaved tree species. *Photosynth. Res.* 67, 229–240.
- Kiesecker, J.M., Blaustein, A.R., Belden, L.K., 2001. Complex causes of amphibian population declines. *Nature* 410, 681–684.
- Li, D.Y., Qiu, G.X., Shen, Y.G., 1982. Some technical problems in using oxygen electrode. *Plant Phys. Commun.* 5, 23–25 (in Chinese with English abstract).
- Longstreth, J.D., de Gruijl, F.R., Kripke, M.L., van der Leun, J.C., 1995. Effects of increased solar ultraviolet radiation on human health. *Ambio* 24, 153–165.
- Madronich, S., McKenzie, R.L., Caldwell, M.M., Björn, L.O., 1995. Changes in ultraviolet radiation reaching the Earth's surface. *Ambio* 24, 143–152.
- Manetas, Y., 1999. Is enhanced UV-B radiation really damaging for plants? Some case studies with European Mediterranean species. In: Rozema, J. (Ed.), *Stratospheric Ozone Depletion: The Effects of Enhanced UV-B Radiation on Terrestrial Ecosystems*. Backhuys Publishers, Leiden, pp. 251–264.
- McKenzie, R.L., Björn, L.O., Bais, A., Ilyas, M., 2003. Changes in biologically active ultraviolet radiation reaching the Earth's surface. *Photochem. Photobiol. Sci.* 2, 5–15.
- Pyle, J.A., 1997. Global ozone depletion: observations and theory. In: Lumsden, P.J. (Ed.), *Plants and UV-B: Responses to Environmental Change*. Society for Experimental Biology, Seminar Series, vol. 64. Cambridge University Press, Cambridge, pp. 3–11.
- Rozema, J., van de Staaij, J., Tosserams, M., 1997. Effects of UV-B radiation on plants from agro and natural ecosystem. In: Lumsden, P.J. (Ed.), *Plants and UV-B: Responses to Environmental Change*. Society for Experimental Biology, Seminar Series, vol. 64. Cambridge University Press, Cambridge, pp. 213–232.
- Rozema, J., van de Staaij, J., Björn, L.O., de Bakker, N., 1999. Depletion of stratospheric ozone and solar UV-B radiation: evolution of land plants, UV-screens and functions of polyphenolics. In: Rozema, J. (Ed.), *Stratospheric Ozone Depletion: The Effects of Enhanced UV-B Radiation on Terrestrial Ecosystems*. Backhuys Publishers, Leiden, pp. 1–20.
- Rozema, J., Björn, L.O., Bornman, J.F., Gaberščik, A., Häder, D.P., Trošt, T., Germ, M., Klisch, M., Gröniger, A., Sinha, R.P., Lebert, M., He, Y.Y., Buffoni-Hall, R., de Bakker, N.V.J., van de Staaij, J., Meijkamp, B.B., 2002. The role of UV-B radiation in aquatic and terrestrial ecosystem—an experimental and functional analysis of the evolution of UV-absorbing compounds. *J. Photochem. Photobiol. B: Biol.* 66, 2–12.
- Searles, P.S., Flint, S.D., Diaz, S.B., Rousseaux, M.C., Ballare, C.L., Caldwell, M.M., 2002. Plant response to solar ultraviolet-B radiation in a southern South American *Sphagnum peatland*. *J. Ecol.* 90, 4704–4713.
- Shi, S.B., Ben, G.Y., Han, F., 1999. Analysis of the solar UV-B radiation and plant UV-B-absorbing compounds in different regions. *Acta Phytoecol. Sin.* 23, 529–535 (in Chinese with English abstract).
- Shi, S.B., Ben, G.Y., Zhao, X.Q., Han, F., 2001. Effects of supplementary UV-B radiation on net photosynthetic rate in alpine plant *Gentiana straminea*. *Acta Phytoecol. Sin.* 25, 520–524 (in Chinese with English abstract).
- Sullivan, J.H., Teramura, A.H., Ziska, L.H., 1992. Variation in UV-B sensitivity in plants from a 3000 m elevation gradient in Hawaii. *Am. J. Bot.* 79, 737–743.
- Tevini, M., Teramura, A.H., 1989. UV-B effects on terrestrial plants. *Photochem. Photobiol.* 50, 479–487.
- Tosserams, M., Rozema, J., 1995. Effects of ultraviolet-B (UV-B) radiation on growth and physiology of the dune grassland species *Calamagrostis epigejos*. *Environ. Pollut.* 89, 209–214.
- Warren, J.M., Bassman, J.H., Eigenbrode, S., 2002. Leaf chemical changes induced in *Populus trichocarpa* by enhanced UV-B radiation and concomitant effects on herbivory by *Chrysomela scripta* (Coleoptera: Chrysomelidae). *Tree Phys.* 22, 1137–1146.
- Zavala, J.A., Scopel, A.L., Ballare, C.L., 2001. Effects of ambient UV-B radiation on soybean crops: impact on leaf herbivory by *Anticarsia gemmatilis*. *Plant Ecol.* 156, 121–130.
- Zhao, X.Q., Zhou, X.M., 1999. Ecological basis of alpine meadow ecosystem management in Tibet: Haibei Alpine Meadow Ecosystem Research Station. *Ambio* 28, 642–647.
- Zhou, X.J., Luo, C., Li, W.L., Shi, J.E., 1995. Changes of total ozone in whole China and its low contents center in Qing-Zang Plateau regions. *Chin. Sci. Bull.* 40, 1396–1398 (in Chinese).
- Zhu, G.L., 1990. Separation and determination of photosynthetic pigments. In: Zhu, G.L. (Ed.), *The Plant Physiological Experiments*. Beijing University Press, Beijing, pp. 51–54 (in Chinese).