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# 云杉幼苗对气候变暖和 UV-B 辐射增强的光合响应

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**摘　要**：采用开顶式有机玻璃罩（OTCs）及紫外灯分别模拟气候变暖和紫外辐射 B(UV-B)增强，对位于气候变暖和 UV-B 增强突出的青藏高原东缘、高山峡谷地云杉（*Picea asperata*）幼苗的光合气体交换和叶绿素荧光参数进行测定分析，探讨云杉幼苗对气候变暖和 UV-B 增强的光合响应特性。结果显示：(1)UV-B 辐射增强显著抑制了云杉幼苗茎和根的伸长生长以及生物量的累积，显著降低了云杉幼苗的净光合速率（$P_n$）、最大光合速率（$P_{max}$）和表观量子产量（$\Phi$），但是提高了光补偿点（$LCP$）；UV-B 辐射增强导致了云杉幼苗光合系统Ⅱ（PSⅡ）的光抑制，使PSⅡ有效量子产量（$\Phi_{PSⅡ}$）显著降低。(2)单纯 OTC 模拟增温显著提高了云杉幼苗的 $P_n$ 和 $P_{max}$，而对气孔导度（$G_s$）、蒸腾速率（$T_r$）和 $\Phi$ 无显著影响。(3)模拟增温缓解了 UV-B 增强对云杉幼苗光合作用的抑制作用，显著提高了 UV-B 胁迫下幼苗的 $P_n$、$P_{max}$、PSⅡ的潜在量子效率（$F_v/F_m$）和有效量子产量（$\Phi_{PSⅡ}$），并且提高了 UV-B 胁迫下幼苗茎、根的生长以及生物量的累积。研究表明，在未来气候变暖和 UV-B 辐射增强同时存在时，气候变暖能够在一定程度上缓解 UV-B 增强对云杉林光合作用的抑制作用。

**关键词**：气候变暖；UV-B 辐射；云杉；光合作用
**中图分类号**：Q945.79　　**文献标志码**：A

# Photosynthetic Responses of *Picea asperata* Seedlings to Climate Warming and Enhanced Ultraviolet-B Radiation

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**Abstract**: Using open-top Chambers(OTCs) and UV-lamps, we manipulated climate warming and enhanced UV-B radiation. The parameters of photosynthetic gas exchange and chlorophyll fluorescence of *Picea asperata* seedlings in the eastern fringe of the Tibetan Plateau, where climate warming and enhanced UV-B radiation(UV-B) were severe, were measured to investigate its photosynthetic responses to the two worsening environmental factors. The results showed that: (1) Enhanced UV-B restrained the net photosynthetic rate ($P_n$), the maximum photosynthetic rate($P_{max}$) and the apparent quantum yield($\Phi$). However, it increased the photosynthetic light compensation point($LCP$). In addition, enhanced UV-B induced photo-inhibition of the photosynthetic system Ⅱ(PS Ⅱ) in *P. asperata* seedlings, and it reduced the effective quantum yield of PS Ⅱ($\Phi_{PSⅡ}$). In the

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end, enhanced UV-B significantly inhibited shoot elongation, root growth and biomass accumulation. (2) OTCs warming significantly enhanced $P_n$ and $P_{max}$, but it had no effects on $G_s$, $T_r$ and $\Phi$. (3) UV-B effects on photosynthesis were amended by warming to some extent, which could be judging from the increased $P_n$, $P_{max}$, intrinsic efficiency ($F_v/F_m$) and $\Phi_{PSⅡ}$ of PSⅡ, and the improved growth. In the end, warming could alleviate the harmful effects of enhanced UV-B on photosynthesis of *P. asperata*.

**Key words**: climate warming; UV-B radiation; *Picea asperata*; photosynthesis

Stratospheric $O_3$ reduction has become one of the pressing concerns about global climate changes, which may result in increases in the level of ultraviolet-B (UV-B) radiation reaching the Earth's surface. It has long been recognized that the increase in UV-B radiation may deleteriously affect plant photosynthesis. There are several direct consequences of UV-B radiation for photosynthesis, which may include photosystem Ⅱ(PS Ⅱ) deactivation[1], photo-destruction of electron transport carriers, and the inhibition of photosynthetic enzymes[2].

Apart from enhanced UV-B, climate warming is another important aspect of global changes which resulting from increased greenhouse gases in air. It is predicted that the increased greenhouse gases will warm global air temperature by about 1.4～5.8 ℃ by the middle of this century with high elevation being especially affected[3]. It is reported that elevated temperature is favorable to growth and photosynthesis in all plants as long as their optimal temperature have not been exceeded[4]. Recently, passive open-top chambers (OTCs) are widely used outdoors and tested effective to simulate climate warming with relatively few influences on other climate factors[5-6].

Under field conditions, plants are usually exposed to several environmental changes simultaneously which may influence them additively, synergistically or antagonistically[7]. *Picea asperata* is a dominant tree species in the southwest of Qinghai-Tibetan Plateau of China and widely used in reforestation program at present. In this region, enhanced UV-B radiation and warming are two prominent aspects of climate changes. Recent reports have shown that ozone is attenuating in this region and a large area of extremely low ozone (190 DU) occurred during December 14～17, 2003[8]. Moreover, it is inferred that responses of vegetation to enhanced UV-B radiation can be modulated by other concomitant changes in growth conditions[9]. Though increasing studies have dealt with the combined effects of environmental changes on plants, few efforts have focused on warming and enhanced UV-B radiation. Moreover, so far, most researches on the combined effects of temperature and enhanced UV-B have carried out under controlled conditions. In the present study, we investigated the combined effects of warming and enhanced UV-B radiation on photosynthesis of *P. asperata* seedlings under field conditions.

## 1 Materials and methods

### 1.1 Experimental design

The experiment was conducted in an open field from April 19 to October 19, 2006 in 301 forestry centre of Miyaluo, Sichuan Province, China (31°35′ N, 102°35′ E, 3 000 m a. s. l.). The study site was located in an open area with homogenous climate factors, especially wind and sunlight, which were closely related to the warming effects of OTCs. The experiment consisted of four treatments: (1) Ambient UV-B with no warming (Control, CK); (2) Ambient UV-B with OTCs warming (W); (3) Enhanced UV-B by 30% with no warming (UV-B); (4) Enhanced UV-B by 30% with OTCs warming (UV-B + W). 12 plot were established, in which warming and UV-B were manipulated with three replicates.

### 1.2 Enhanced UV-B and warming treatment

Followed by the International Tundra Experiment, warming was manipulated by open-top chambers (OTCs) constructed with pure Plexiglas boards (3 mm thick) without addition of UV-absorbing compounds (PLEXIGLAS®, Evonik-Degussa, made in Shanghai, China, Essen, Germany), which maintained near-natural transmittance of visible wavelengths (>92%) and low transmittance of reradiated infrared wavelengths (<5%). The OTCs were hexagonal in shape with

1.27 $m^2$ (at the top) and 2.10 $m^2$ (at the base) in area, and 65 cm in height.

Supplemental UV-B was artificially provided by UV-B fluorescent lamps (Beijing Electronic Resource Institute, Beijing, China) with 40 cm in length and 40 W in power rating. In enhanced-UV-B frames, lamps were wrapped with 0.10 mm cellulose diacetate film, which transmitted both UV-B(290～315 nm) and UV-A (315～400 nm). In ambient-UV-B frames, lamps were wrapped with 0.125 mm polyester film (Chenguang Research Institute of Chemical Industry, Chengdu, China), which transmitted only UV-A radiation (315～400 nm). All plots also received natural solar radiation. Films were replaced weekly. That was both UV-B-control plots and enhanced-UV-B plots received similar elevated-UV-A radiation. UV-lamps worked for 8 h daily centered on the solar noon. Constant distances of 95 cm from the lamps to the apex of plants were kept throughout the experiment to maintain the specified UV-B levels, and the lamps were replaced in time. The UV-irradiance at the apex of the plant canopy under the lamps was determined with an Optronics Model 742 (Optronics Laboratory Inc., Orlando, FL) spectroradiometer and the spectral irradiance was weighted according to the generalized plant action spectrum and normalized at 300 nm to obtain effective radiation ($UV\text{-}B_{BE}$). The supplemental UV-B radiation was 3.71 $kJ \cdot m^{-2} \cdot d^{-1}$ ($UV\text{-}B_{BE}$) and the ambient UV-B radiation was 12.64 $kJ \cdot m^{-2} \cdot d^{-1}$ ($UV\text{-}B_{BE}$).

### 1.3 Materials

Indigenous soil of each plot until the depth of 35 cm was replaced by the topsoil from a local spruce-forest which was sieved and mixed well. In a preliminary experiment, the soil depth did not affect seedling root growth during a 2-year growth period. Two-year-old *P. asperata* seedlings from a local nursery with uniform plants height, basal diameter and fresh weight were transplanted into each plot with a single line under each lamp. The plant height, basal diameter and whole-plant fresh weight at the beginning of the experiment were (6.31±0.42) cm, (1.72±0.21) mm and (1.69±0.18) g, respectively. Seedlings were planted in the center of each plot, and perpendicularly below the UV-lamps with 35 cm between lines and 15 cm between seedlings. The seedlings were watered as needed.

### 1.4 Temperature and soil moisture measurement

To estimate warming effects of OTCs, air (10 cm above soil surface) and soil temperatures (5 cm depth), and air relative humidities were measured between OTCs and Control plots. Temperatures were continuously measured at two hours intervals from April 19 to October 19, 2006 using sensors connected to data-logger (Campbell AR5, Avalon, USA). Soil moisture in 20 cm was measured in soil core samples collected twice each month at all plots. The soil was dried at 105 ℃ for 12 h to determine soil moisture.

### 1.5 Parameter analysis

**1.5.1 Gas exchange** After three months of treatment, the net photosynthetic rate ($P_n$, $\mu mol \cdot m^{-2} \cdot s^{-1}$) of the current-year, fully expanded needles in all the treatments were measured under controlled optimal conditions using a portable photosynthesis system (Li-6400, Lincoln, NE, USA) in the open circuit mode. The photon flux density (PFD) was maintained at ca. (1 000 ±50) $\mu mol \cdot m^{-2} \cdot s^{-1}$ using the 6 400 artificial light source, and temperature was maintained at (25±1.5) ℃ with an *RH* of 36%～55% inside the leaf chamber during measurement. The $CO_2$ concentration was maintained at (360±10) $\mu mol \cdot mol^{-1}$. Measurements were made between 9:00 and 10:30. Needles were arranged in the cuvette such that self-shading was minimized and all needles were paralled to the plane of the leaf chamber. The projected area of the measured needles was estimated using measurements of needle length and width.

**1.5.2 $P_n$-PAR response curve** All measurements were made in the same sampling method as described above. The block temperature was held at 20 ℃ and the relative humidity at 40%. The response to *PAR* were measured at 0, 20, 50, 80, 100, 200, 400, 600, 800, 1 000, 1 200, 1 500, 1 800, and 2 000 $\mu mol \cdot m^{-2} \cdot s^{-1}$. The light-response curve of photosynthesis was fitted with a non-rectangular hyperbola[10]. Where $P_n$ is the net photosynthetic rate, $\Phi$ is the initial slope of the curve, $I$ is the PPFD, $P_{max}$ is the light-saturated rate of photosynthesis, $\theta$ is the convexity and $R_d$ is the dark respiration rate. First, from linear regression of the net photosynthetic rate on PPFD at 0～200 μmol · $m^{-2}$ · $s^{-1}$, $\Phi$ and *LCP* were obtained as the slope, *y*-intercept and the *x*-intercept of these regressions, respectively. Then, a non-rectangular hyperbolawas fitted to the whole curve using the $\Phi$ and $R_d$ values to obtain $P_{max}$ and $\theta$[11].

**1.5.3 Chlorophyll fluorescence** Chlorophyll fluorescence measurements were taken on the same leaves with gas exchange measure using a modulated fluorometer (PAM-2100, Walz, Effeltrich, Germany), as described by Brugnoli and Björkman[12]. The leaves were pre-darkened at least for 30 min before measuring. The intensity of the saturation pulse to determine the maximal fluorescence emission in the presence($F_m'$) and in the absence($F_m$) of quenching on the upper surface of the leaf was 8 000 μmol · $m^{-2}$ · $s^{-1}$. The "actinic light" was 600 μmol · $m^{-2}$ · $s^{-1}$. The fluorescence parameters were determined according to Rosenqvist and van Kooten[13].

**1.5.4 Growth parameter measurement** At the end of the experiment, the plant height and basal diameter were measured and the seedlings were harvested. Then, the seedlings were divided into needle, root and stem. All the organs were dried at 80 ℃ for 1 week and weighed.

### 1.6 Statistical analysis

All data were analyzed using a two-way analysis of variance(ANOVA) to test the UV-B, warming and UV-B×warming interaction effects. $P_n$-PAR response curves were fitted using linear regression and non-linear regression. All statistical analyses were performed using the Software Statistical Package for the Social Science(SPSS) version 11.5 for windows statistical software package(SPSS Inc., Chicago, Illinois).

## 2 Results and analysis

### 2.1 Effects of enhanced UV-B and warming on temperature and humidity in air and soil

OTCs significantly increased the air and soil temperatures on average 1.74 ℃ and 0.92 ℃, respectively (Table 1). Air relative humidity was decreased by 3.12% and 3.99% in W and UV-B+W treatments compared with their respective controls. Soil moisture was also lower on average 2.01% and 2.53% in W and UV-B+W treatments than their respective controls. However, there were no significant differences between treatments in air relative humidity and soil moisture. Enhanced UV-B also did not significantly affect soil moisture during the study period.

### 2.2 Effects of enhanced UV-B and warming on growth

Supplemental UV-B markedly inhibited shoot elongation and biomass accumulation, and reduced root/shoot ratio of *P. asperata* seedlings despite of temperature levels (Table 2). OTCs warming significantly stimulated shoot growth in spite of UV-B levels. Moreover, it improved shoot elongation, root growth and total biomass accumulation under enhanced UV-B. Significant UV-B×warming interaction was detected on total biomass. OTCs warming markedly improved biomass accumulation under enhanced UV-B, however, the effect was not significant under ambient UV-B.

### 2.3 Effects of enhanced UV-B and warming on gas exchange parameters and properties from photosynthetic light response curves

Enhanced UV-B caused decreases in the net photosynthetic rate($P_n$), the stomata conductance to vapor($G_s$) and the transpiration rate ($T_r$), but

**Table 1 The effects of OTCs on daily mean temperature, air relative humidity, and soil moisture from April 19 to October 19, 2006**

| Environmental parameter | Treatment | | | |
|---|---|---|---|---|
| | CK | UV-B | W | UV-B+W |
| Air temperature/℃ | 16.65±0.33b | 16.73±0.27b | 18.33±0.43a | 18.52±0.13a |
| Soil temperature/℃ | 15.31±0.19b | 15.23±0.17b | 16.25±0.17a | 16.13±0.13a |
| Airrelative humidity/% | 73.22±1.61a | 72.95±0.68a | 70.06±2.40a | 68.96±2.44a |
| Soil moisture/% | 20.03±1.68a | 19.72±0.70a | 18.02±1.48a | 17.19±1.21a |

Note: Values were the mean±SE of 3 replicates for temperature and air relative humidity, and 6 replicates for soil moisture. The different normal letters in the same column indicates significant difference between two treatments at 0.05; The same as below.

increased the intercellular $CO_2$ concentration($C_i$) in *P. asperata* seedlings irrespective of temperature levels(Fig. 1). Furthermore, the maximum photosynthetic rate($P_{max}$), the apparent quantum yield ($\Phi$), and the dark respiration rate($R_d$) were reduced, but the photosynthetic light compensation point($LCP$) was heightened by supplemental UV-B in seedlings either under ambient temperature or under OTCs warming(Fig. 2). OTCs warming significantly increased $P_n$ and $P_{max}$ in spite of UV-B levels. Under warming, seedlings exposed to enhanced UV-B radiation exhibited higher $P_n$, $P_{max}$ and $\Phi$, but lower $LCP$ than those under no warming. UV-B×warming interactive effects were significant in $C_i$, $LCP$ and $\Phi$.

### 2.4 Effects of enhanced UV-B and warming on parameters of chlorophyll fluorescence

The markedly increased minimal fluorescence($F_0$) and non-photochemical quenching coefficient ($NPQ$) were induced by supplemental UV-B radiation in spite

**Table 2 The effects of enhanced UV-B and warming on growth of *P. asperata***

| Growth parameters | Treatment | | | |
|---|---|---|---|---|
| | CK | UV-B | W | UV-B+W |
| Height/cm | 9.49±0.35b | 7.46±0.35d | 12.13±0.40a | 8.48±0.36c |
| Root weight/g | 0.35±0.03a | 0.19±0.03c | 0.37±0.03a | 0.27±0.02b |
| Total biomass/g | 1.04±0.04a | 0.71±0.04c | 1.07±0.04a | 0.91±0.04b |

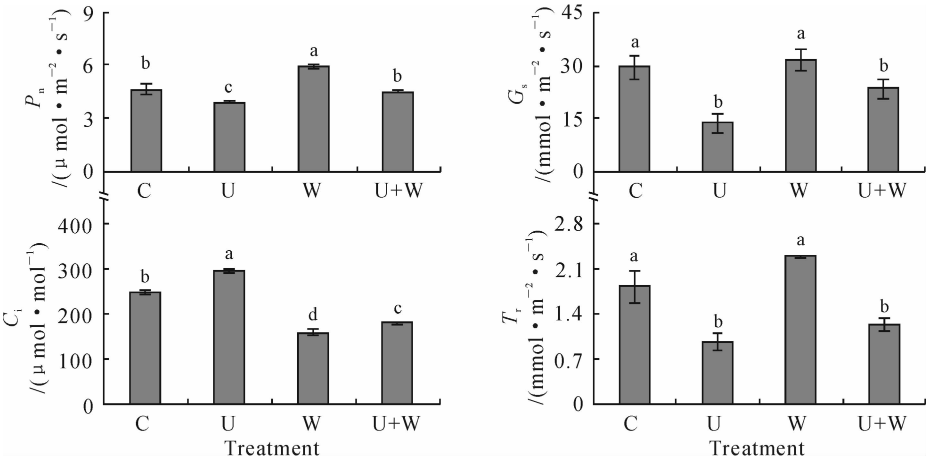

Fig. 1 The parameters of photosynthetic gas exchange affected by enhanced UV-B and OTCs warming

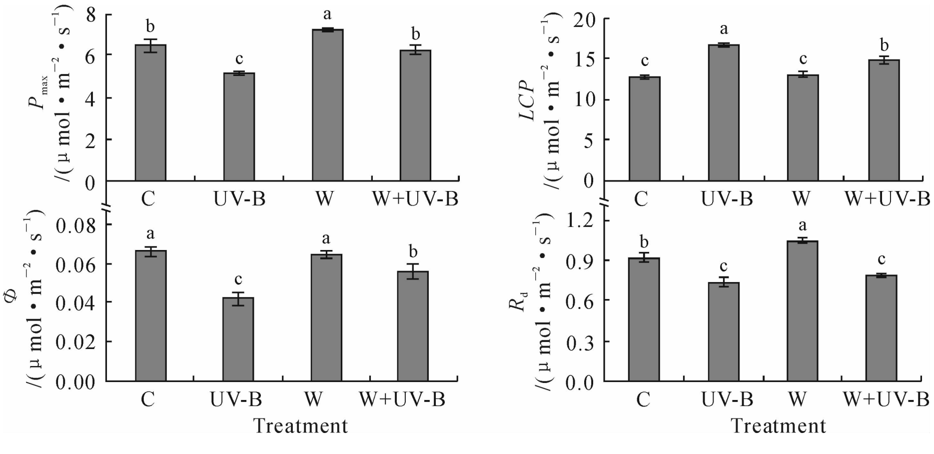

Fig. 2 The maximum net photosynthetic rate($P_{max}$), the apparent quantum yield($\Phi$), the dark respiration rate($R_d$), and the photosynthetic light compensation point($LCP$) of *P. asperata* seedlings affected by enhanced UV-B and OTCs warming

**Table 3　The effects of enhanced UV-B and warming on chlorophyll fluorescence of *P. asperata***

| Chlorophyll fluorescence | Treatment | | | |
|---|---|---|---|---|
| | CK | UV-B | W | UV-B+W |
| $F_0$ | 0.24±0.00b | 0.26±0.00a | 0.22±0.01c | 0.24±0.01 b |
| $F_v/F_m$ | 0.84±0.01a | 0.67±0.03c | 0.81±0.01ab | 0.76±0.03 b |
| $NPQ$ | 0.34±0.01c | 0.65±0.01a | 0.36±0.01c | 0.47±0.02 b |
| $\Phi_{PS II}$ | 0.55±0.02a | 0.28±0.02d | 0.44±0.02 b | 0.35±0.01 c |

of temperature levels (Table 3). Furthermore, supplemental UV-B also reduced the effective quantum yield of PS Ⅱ ($\Phi_{PS II}$) across temperature treatments. Enhanced UV-B decreased the intrinsic efficiency of PS Ⅱ ($F_v/F_m$) in seedlings exposed to ambient temperature, but this effect was insignificant in those under warming. There were no significant differences in $F_v/F_m$ and $\Phi_{PS II}$ between temperature treatments. The interactive effects of UV-B × warming were detected in $F_v/F_m$, $NPQ$ and $\Phi_{PS II}$.

## 3　Discussion

Employing OTCs in global warming studies was evaluated and validated by Hollister and Webber[14]. The open-top design of OTCs also allows free air exchange and minimizes most undesirable ecological effects, including lower light levels, temperature extremes, unnatural precipitation, $CO_2$ concentrations, unnatural gas concentrations and humidity problems[14]. OTCs were tested to elevate mean air temperature (13 cm height) by on average 0.6～2.2 ℃ during the growth season[15]. Jones *et al*. reported OTCs warmed soil (3 cm depth) temperature by 1.8 ℃[16]. In present investigation, OTCs warmed mean air and soil temperatures by 1.74 ℃ and 0.92 ℃, respectively, throughout the growing season. Our results showed that OTCs did not significantly affect soil moisture and air relative humidity, and the same conclusion was also drawn by other research[17].

Photosynthesis is of primary importance for biomass production. Accordingly, it is likely that UV-B-induced disturbances in photosynthetic reactions can cause reduction in biomass and yield[18]. Our study revealed that supplemental UV-B reduced the photosynthetic capacity of *P. asperata* seedlings, which could be seen from the decreased net photosynthetic rate ($P_n$), maximum photosynthetic rate ($P_{max}$), and apparent quantum yield ($\Phi$). Moreover, the negative effects of enhanced UV-B on photosynthetic processes have also been demonstrated by other research[19]. On the other hand, an increase in the intercellular $CO_2$ concentration ($C_i$), and reductions in the transpiration ($T_r$) and the stomatal conductance to vapor ($G_s$) were detected in seedlings under enhanced UV-B in the present investigation. The reduced $G_s$, and hence decreased E, were probably a function of increased $C_i$ resulting from the inhibited capacity for $CO_2$ fixation[20]. $C_i$ can be used to discriminate between changes in $P_n$ resulting from stomatal limitation or non-stomatal limitations[21]. Our result further confirmed that the drop in $P_n$ due to supplemental UV-B was more closely related to non-stomata than to stomata limitations. It was reported that enhanced temperature in the short term could stimulate photosynthesis until the optimum temperature was reached[22]. In this study, OTCs warming also advanced the photosynthetic rate. Moreover, it offset the harmful effects of enhanced UV-B on photosynthesis judging from the increased $P_n$, $P_{max}$ and $\Phi$ compared with under single UV-B stress, as might be one of the reasons for its ease effects on the growth of *P. asperata* seedlings under UV-B stress.

The chlorophyll fluorescence signatures provide basic information on the function of photosynthetic apparatus, and on the capacity and performance of photosynthesis. In chloroplast study, photosynthetic system Ⅱ (PS Ⅱ) is extremely vulnerable to UV-B radiation with pigments, cofactors and proteins being modified[23]. Moreover, photo-inhibition due to UV-B radiation may also additionally decrease the net photosynthesis[24]. The intrinsic or maximum efficiency of PS Ⅱ ($F_v/F_m$) and the minimal fluorescence ($F_0$) are accepted and widely used as reliable diagnostic indicators of photo-inhibition[25]. Decreased $F_v/F_m$ and increased $F_0$ are used for indicating the occurrence of photo-inhibition damage in response to stress, and our result was consistent with them. Furthermore, reduction in $F_v/F_m$ may associate with direct damage by enhanced UV-B to PS Ⅱ[26] or alteration of the xanthophylls cycle[27]. The change in the non-photochemical quenching ($NPQ$)

measures a change in the efficiency of heat dissipation and in the present investigation, reduced *NPQ* was detected under enhanced UV-B. The effective quantum yield of PS Ⅱ ($\Phi_{\mathrm{PS\,II}}$) measures the proportion of the light absorbed by chlorophyll associated with PS Ⅱ that is used in photochemistry. As such, it can give a measure of the rate of linear electron transport and so an indication of overall photosynthesis. Enhanced UV-B in our study caused a reduction in $\Phi_{\mathrm{PS\,II}}$, which revealed that enhanced UV-B decreased the photochemical efficiency of PS Ⅱ. From our result, UV-B-induced inhibited photosynthetic capacity was accompanied by photo-inhibition and the decrease in the photochemical efficiency of PS Ⅱ. It was reported that enhanced UV-Binhibited photosynthetic capacity without any damage to PS Ⅱ[28]. Shawna *et al.*, however, reported that increased UV-B radiation caused a significant decrease in the photochemical efficiency of PS Ⅱ[29]. For many years PS Ⅱ is considered as the most temperature-sensitive step in photosynthesis, but it appears from numerous reports that PS Ⅱ inhibition does not occur until leaf temperature are quite high, usually 40 ℃ and above[30]. In our study, OTCs warming had no significant effects on PS Ⅱ, but it lowered the risk of photo-inhibition and heightened the photochemical efficiency of PS Ⅱ in seedlings under enhanced UV-B, which might explain its easing effects on UV-B-induced inhibited photosynthetic ability.

In conclusion, enhanced UV-B reduced the capacity of photosynthesis in *P. asperata* seedlings in one growing season. UV-B-induced photo-inhibition of PS Ⅱ and the decreased $\Phi_{\mathrm{PS\,II}}$ may explain the reduced photosynthesis to some content. On the other hand, OTCs warming favored the photosynthesis of seedlings under ambient UV-B, and it also reduced the photosynthetic sensitivity of *P. asperata* seedlings to UV-B stress.

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