Abstract. Ultraviolet-A (UV-A) is the main component of UV radiation in nature. However, its role on plant growth, to a large extent, remains unknown. In this study, tomato (Solanum lycopersicum ‘Beijing Cherry Tomato’) seedlings were cultivated in an controlled environment in which UV-A radiation was provided by UV-A fluorescent lamps ($\lambda_{\text{max}} = 369$ nm) with a fluence rate of $2.28 \text{ W} \cdot \text{m}^{-2}$. The photoperiod of UV-A radiation was 0, 4, 8, and 16 hours, which corresponds to control, UV-A4, UV-A8, and UV-A16 treatments, respectively. The photosynthetic photon flux density (PPFD) was $220 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, which was provided by light-emitting diodes (LEDs) with a blue/red light ratio of 1:9; the photoperiod of PPFD was 16 hours. We showed that supplementing 8 and 16 hours of UV-A to visible radiation (400–700 nm) stimulated plant biomass production by 29% and 33%, respectively, compared with that of control. This resulted mainly from larger leaves (i.e., 22% and 31% in 8 and 16 hours UV-A, respectively), which facilitated light capture. Supplemental UV-A also enhanced photosynthetic capacity, as indicated by greater net photosynthesis rates in response to CO$_2$ under saturating PPFD. Furthermore, the greatest stomatal conductance ($g_s$) value was observed in UV-A16, followed by UV-A8, which correlated with the greater stomatal density in the corresponding treatments. Moreover, supplemental UV-A did not induce any stress, as the maximum quantum efficiency of photosynthetic system II (PSII) ($F_{v}/F_{m}$) remained ~0.82 in all treatments. Similarly, chlorophyll content and leaf mass area (LMA) were also unaffected by UV-A radiation. Taken together, we conclude that supplementing reasonable levels of UV-A to visible radiation stimulates growth of indoor cultivated tomato seedlings.
The flow rate was 500 mmol·m⁻²·s⁻¹, vapor pressure deficit was 0.7 to 1.0 kPa, and the leaf temperature was 25°C. During the measurements, the CO₂ partial pressure was 400 mmol·m⁻²·s⁻¹.

For measuring leaf photosynthesis (Aₚ), in response to PPFD, the leaves were first adapted to the cuvette at 1500 mmol·m⁻²·s⁻¹ PPFD until Aₚ and gₛ became stable, and a measurement was recorded. Then, they were exposed to 1200, 900, 600, 400, 300, 200, 100, 50, and 0 mmol·m⁻²·s⁻¹ PPFD. At each PPFD, measurements were taken when Aₚ reached a steady state (after about 5–10 min). The data were fitted to the nonrectangular hyperbola model of Thornley (1976), which estimated the maximum photosynthesis rate at saturating light, the light-limited quantum yield for CO₂ fixation, and the dark respiration.

For determination of Aₚ in response to CO₂, the leaves were acclimated to 1500 mmol·m⁻²·s⁻¹ PPFD and 400 μbar CO₂, until Aₚ and gₛ were stable, and a measurement was recorded. Thereafter, leaves were exposed to a range of CO₂ partial pressures: 300, 200, 150, 100, 50, 400, 600, 800, 1000, 1200, and 1500 μbar. At each CO₂ level, measurements were taken when Aₚ reached a steady state (after about 3–5 min for each step). Data from CO₂ response curves were corrected for leaks of CO₂ into or out of the cuvette by using photosynthetically inactive leaves (Flexas et al., 2007). Aₚ as a function of intercellular CO₂ partial pressure (Cᵢ) was fitted through the model of Sharkey et al. (2007), which estimated the maximum carboxylation rate of ribulose 1, 5-bisphosphate carboxylase/oxygenase, Rubisco; the maximum rate of photosynthetic electron transport, and triose phosphate use.

During gas exchange measurements, chlorophyll fluorescence parameters (Fᵢ′, maximum fluorescence yield of a light-adapted leaf; Fᵢ, fluorescence under actinic light; and F₀′, minimum fluorescence yield of a light-adapted leaf) were recorded simultaneously. Maximum and minimum fluorescence yield of dark-adapted leaves (F₀, and F₀′, respectively) were measured with the leaves fully dark adapted for a whole night. Detailed settings for the fluorescence measurements followed those of Zhang et al. (2018). Based on these data, the quantum efficiency of PSII (ΦPSII), and Fᵢ/Fᵢ′ were estimated according to Baker (2008).

**Stomatal conductance.** Stomatal conductance was measured with a porometer (model AP4; Delta-T Devices, Cambridge, UK). Four plants were selected randomly from each treatment as four replicates. One leaflet of the fourth leaf from the bottom of the plant was selected, and the measurements were done in situ when UV-A lamps were turned on in all treatments (i.e., from 1300 to 1500 μm). Stomatal conductance was recorded in four different positions in each leaf blade, which were considered as four technical replicates, and the mean value of four technical replicates was considered as one biologic replicate.

**Leaf optical properties.** Leaf reflectance and transmittance were measured within the visible spectrum (400–700 nm) with a spectroradiometer (USB2000+; Ocean Optics, Largo, FL) in combination with two integrating spheres (FOIS-1 and ISP-REF, Ocean Optics). Leaf absorbance (Aₐ) was calculated as Aₐ = 1 − (Rₚ + Tₚ), where Rₚ and Tₚ are the reflectance and transmittance of leaf samples, respectively. For determination of chlorophyll a and b contents, acetone (80%) was used as the solvent, and the absorbance of the extracts was measured using a UV/Vis spectrophotometer (model UV-1800; Shimadzu, Kyoto, Japan). The chlorophyll concentrations were calculated using the equations derived by Wellburn (1994). Stomatal density was determined according to Zhang et al. (2018).

**Statistical analysis.** The effects of UV-A on plant growth and physiologic traits were evaluated by analysis of variance followed by Fisher’s protected least significant difference test at 95% confidence with R 3.4.0 (R Foundation for Statistical Computing, Vienna, Austria). The four destructive measurements were considered as four blocks in statistical analysis. P values less than 0.05 were regarded as significantly different.

**Results.**

The growth of tomato seedlings showed a positive response to supplemental UV-A radiation (Fig. 2). Specifically, supplementing 8 and 16 h of UV-A to visible radiation stimulated plant biomass production by 29% and 33%, respectively, compared with that of the control. Such a stimulating effect did not occur in the treatment of 4-h UV-A supplementation (Fig. 2A). A similar effect was observed for plant leaf area, which was 22% and 31% greater in the UV-A8 and UV-A16 treatments, respectively, compared with the control (Fig. 2B). Stem length was also stimulated by supplemental UV-A radiation, although the tallest plants were seen in the UV-A8 treatment (Fig. 2C).

The response of Aₚ and ΦPSII to PPFD were unaffected by UV-A radiation (Fig. 3A and C; Table 2). However, supplemental UV-A remarkably affected the response of Aₚ and ΦPSII to Cᵢ. Specifically, plants grown in the UV-A8 and UV-A16 treatments displayed greater Aₚ and ΦPSII than the other treatments, particularly under greater CO₂ concentrations (Fig. 3B and D), whereas plants in

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**Table 1. Lighting characteristics of the four ultraviolet-A treatments.**

| Treatment       | Photoperiod of ultraviolet-A (hr) | Daily ultraviolet-A dose (kJ·m⁻²·d⁻¹) | Daily PPFD integral (mol·m⁻²) |
|-----------------|-----------------------------------|---------------------------------------|------------------------------|
| Control         | —                                 | —                                     | 12.67                        |
| Ultraviolet-A4  | 1200–1600                         | 0.58                                  | 12.67                        |
| Ultraviolet-A8  | 1000–1800                         | 1.17                                  | 12.67                        |
| Ultraviolet-A16 | 0600–2200                         | 2.34                                  | 12.67                        |

*Daily ultraviolet-A dose was weighed by using a biologic spectral weighing function according to Flint and Caldwell (2003). PPFD = photosynthetic photon flux density ( photon flux integral between 400 and 700 nm, measured in micromoles per square meter per second).
the UV-A4 treatment had a similar photosynthetic capacity as that of the control (Fig. 3B).

Plants grown under different UV-A doses showed substantial differences in gs (Fig. 4), which was greatest in the UV-A16 treatment, followed by UV-A8, and it was similar between the treatment of UV-A4 and the control. Corresponding to gs, the effect of UV-A on stomatal density was also significant (Table 3). With regard to the adaxial side of the leaf, stomatal density in the UV-A8 and UV-A16 treatments was higher than the other treatments. With regard to the abaxial side, a significant difference was seen only between the UV-A8 and UV-A4 treatments, which showed the greatest and least values, respectively.

Leaf absorptance spectra of all treatments were similar in most parts of the visible waveband (400–700 nm), except in the green region (530–580 nm). In the green spectrum, absorptance was greatest and least values, respectively.

**Discussion**

Adding UV-A to visible radiation in a controlled environment accelerates the growth of tomato seedlings significantly, as showed by the 29% to 33% enhancement in total plant biomass in our study (Fig. 2A), which is contrary to the effect of UV-B, which often represses plant growth (Tsormpatsidis et al., 2008). This is in consistent with previous studies carried out either in greenhouse or in open field conditions with cutoff filters or supplemental UV-A radiation (Bernal et al., 2015; Tezuka et al., 1993). However, some studies indicated that plant biomass was reduced by UV-A radiation (Baroniyaa et al., 2013; Krizek et al., 1998). Such a discrepancy in plant growth in response to UV-A radiation remains ambiguous because the information regarding the effect of UV-A on plant biomass production is limited. Verduguet al. (2017) proposed that the variable UV-A responses may be caused by small changes in the balance between multiple, simultaneous UV-A effects, including induced stress, changes in morphology and photosynthesis, as well as accumulation of phenolic compounds with antioxidative capabilities. Furthermore, it has been reported that some effects of UV-A on biomass accumulation are modulated by other environmental factors (Bernal et al., 2013). Nevertheless, this may not play a role in our study as all environmental factors were kept constant except irradiance.

Light interception correlates closely with the morphology of shoots, which is one of the driving forces behind plant photosynthesis (Sarlikioti et al., 2011). Previous studies demonstrated that UV-A stimulates leaf elongation in beans (Antonelli et al., 1997). This is in line with our study in which supplemental UV-A radiation increased total leaf area by 22% to 31% (Fig. 2B). The larger leaves facilitated light capture and, consequently,
contributed to biomass production (Fig. 2A). Although detailed information about the way that UV-A radiation mediates leaf expansion is lacking, UV-A exposure may upregulate the expression of cry1A (Mariz-Ponte et al., 2018), as cry-impaired plants have exhibited significantly smaller leaf blades (Kozuka et al., 2005). Thus, it is assumed that upregulation of cry1A by UV-A promotes leaf expansion (Mishra and Khurana, 2017). In addition to leaf size, plant height was also slightly increased by UV-A radiation (Fig. 2C), and a similar phenomenon has been noted in some Sorghum bicolor varieties (Kataria and Guruprasad, 2012). Such effects have been attributed to blue/UV-A absorbing cry1A proteins, which can play a role in shade avoidance (Keller et al., 2011). However, there are also studies that reported that UV-A radiation decreased plant height (Düder et al., 2014; Rechner et al., 2017). In this context, more evidence is needed to corroborate speculations about UV-A radiation playing a functional role in countering the shade-acclimated phenotype.

Plant growth processes often exhibit a saturation response to growth irradiance (Taiz and Zeiger, 2006). In the current study, although the UV-A radiation level in the UV-A8 treatment was half of that in the UV-A16 treatment, the total leaf area and biomass production in the UV-A8 treatment were similar, as in the UV-A16 treatment (Fig. 2), which indicates that plant growth may show a saturation response to UV-A radiation level. Moreover, compared with 8 and 16 h of supplemental UV-A, 4 h of supplemental UV-A hardly affected plant growth and leaf expansion (Fig. 2). This is probably results from the fact that 4 h of supplemental UV-A radiation was not enough to induce the stimulation of plant growth, as the UV-A radiation level in the UV-A4 treatment was only ≈8% of the average UV radiation in nature (Liu et al., 2017). Therefore, our results indicate that UV-A radiation may affect plant growth qualitatively, but detailed studies are needed to elucidate its mechanisms.

Plant photosynthesis is highly sensitive to its prevailing growth environment. Conventionally, the UV component of solar radiation has been considered to be detrimental to photosynthesis, as UV radiation induces the degradation of D1 and D2 proteins in the photosynthetic apparatus, and consequent destruction of PSII (Christopher and Mullet, 1994; Greenberg et al., 1989). However, the maximum quantum efficiency of PSII photochemistry was unaffected by UV-A radiation in our study, as reflected by the similar $F_v/F_m$ values (≈0.82) among the treatments (Table 3), which indicates that plants were not stressed with a well-functioning photosynthetic apparatus. Furthermore, the net photosynthesis rate in response to PPFD was also unaffected by UV-A (Fig. 3A), which correlates with the same response of $F_\text{PSII}$ at different PPFD (Fig. 3C). This is not surprising because previous studies have shown that, under low light or nonsaturating background PPFD (e.g., 500 μmol·m$^{-2}·s^{-1}$), UV-A radiation did not affect the functions of the photosynthetic apparatus and even enhanced photosynthetic rates (Mantha et al., 2001). This is further confirmed by the UV-A-acclimated plants showing greater net photosynthesis rates in response to CO$_2$ under saturating PPFD (Fig. 3B). Our results indicate that reasonable levels of UV-A increase the potential of photosynthetic capacity, but this might not attribute to the biomass accumulation as plants were grown under ambient CO$_2$ and low PPFD in this study.

Light is one of the key stimuli for regulating stomatal traits. The significantly greater $g_s$ in the UV-A8 and UV-A16 treatments correlated with the corresponding greater stomatal density (Fig. 4; Table 3). Furthermore, it has also been proposed that the greater $g_s$ under UV-A radiation might be a result of increased stomatal opening, which is caused by the absorption of UV-induced blue/green fluorescence by cryptochromes located in stomata (Mantha et al., 2001). The greater $g_s$ can decrease the diffusion limitation of CO$_2$ into the leaf and facilitate carbon assimilation. Apart from $g_s$, leaves grown under a greater supplemental UV-A dose showed an increased absorptance in the green region of the spectra (Fig. 5). It has been reported that anthocyanins absorb light in the green region of the spectra (Merzlyak et al., 2008), which was supported by the work of Gitelson et al. (2001) with maple leaves. Hence, plants grown under supplemental UV-A radiation probably have a greater anthocyanin concentration.

Although UV-A radiation is rarely applied in indoor cultivation systems compared with other parts of the spectra, we have shown that allowing reasonable levels of UV-A radiation in a controlled environment boosts the growth of tomato seedlings. The results shown here may provide a direction for optimizing a light recipe for indoor cultivation.

**Conclusions**

We conclude that UV-A radiation stimulates growth of tomato seedlings in indoor cultivation, as indicated by greater biomass production, which resulted mainly from the larger expansion of leaf area that facilitated light capture. This stimulating effect exhibited a saturation response to the UV-A dose.

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