

UVA radiation promotes tomato growth through morphological adaptation leading to increased light interception



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ABSTRACT

UVA radiation (315–400 nm) is the main component of solar UV radiation. Although it shares photoreceptors (i.e. cryptochromes and phototropins) with blue light (400–500 nm), its function in plant biology is unclear to a large extent. This study aimed at exploring how UVA radiation affects plant morphology and physiology, and at distinguishing to what extent these effects differ from those of blue light. Tomato plants were grown under monochromatic red (R), dichromatic red and blue (R/B = 7:1), as well as red and two different levels of UVA radiation (R/UVA = 7:1 and 15:1, respectively), with identical photon flux density ($250 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). Peak intensities of UVA, B and R were 370, 450 and 660 nm, respectively. We showed that replacing blue by UVA (in a background of red light) induced plant morphological modifications, as reflected by larger leaf area, steeper leaf angles, flatter leaves and longer stems. UVA had reduced effects on leaf secondary metabolism compared to blue light, resulting in significantly lower total phenolics and flavonoid contents, as well as concentrations of UV-absorbing compounds. In addition, UVA had a similar function as blue light in shaping the development of the photosynthetic apparatus, as both wavebands alleviated the ‘red light syndrome’ (i.e. low photosynthetic capacity, reduced photosynthetic electron transport, and unresponsive stomata). We conclude that: 1) UVA promotes tomato growth through morphological adaptation leading to increased light interception; 2) UVA affects leaf secondary metabolite accumulation less strongly than blue light; 3) UVA functions similarly to blue light in maintaining leaf photosynthetic functioning. Thus, unlike previously suggested, UVA cannot be unequivocally considered as an abiotic stress factor. This research adds to the understanding of plant processes in response to UVA radiation and provides a basis for future recipes for growing plants with artificial light.

1. Introduction

Plants use multiple photoreceptors to detect light cues in a broad waveband: for example, phytochromes are specifically red and far-red light sensitive (Quail et al., 1995; Smith, 2000), while cryptochromes and phototropins are sensitive to blue and UVA radiation (Ahmad and Cashmore, 1993; Kang et al., 2008; Galvao and Fankhauser, 2015). Blue light is involved in a wide range of plant developmental processes such as photomorphogenesis (Folta et al., 2003; Inoue et al., 2008; Pedmale

et al., 2016) and leaf photosynthetic development (Matsuda et al., 2004; Hogewoning et al., 2010). UVA (315–400 nm) is the main component of solar UV radiation reaching the Earth's surface (Brune et al., 2001). Although it shares photoreceptors with blue light (400–500 nm), its function in plant biology is unclear to a large extent (Verdaguer et al., 2017; Neugart and Schreiner, 2018). Compared with other wavebands (e.g. UVB, far-red, red and blue), studies on UVA effects on plant growth are limited and the results are often contradictory (Verdaguer et al., 2017). For instance, UVA has been suggested to

Abbreviations: SAS, shade avoidance syndrome; SLA, specific leaf area; IAA, auxin; BR, brassinosteroid; Ab, light absorbance; Rf, reflectance; Tr, transmittance; Chl, chlorophyll; g_s , stomatal conductance; F_m and F_o , maximal and minimal fluorescence; F_s , fluorescence under actinic light; F_m' and F_o' , maximal and minimal fluorescence yield in the light-adapted state; F_v/F_m , maximum quantum efficiency of PSII; LEDs, light emitting diodes; NPQ, non-photochemical quenching; A_{max} , maximum net leaf photosynthetic rate; PFD, photon flux density; PPFD, photosynthetic photon flux density; PSII, photosystem II; Φ_{PSII} , PSII operating efficiency; qP, photochemical quenching; R_d , dark respiration rate; α , Photosynthetic quantum yield; $\text{VPD}_{\text{leaf-air}}$, leaf-to-air vapor pressure deficit; RUE, rutin equivalent; GAE, galic acid equivalent

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promote plant growth (Maffei et al., 1999; Kang et al., 2018), while other studies reported the opposite (Baroniya et al., 2014; Zhang et al., 2014). Moreover, in many studies, UVA radiation was supplied as supplemental to broad-range visible radiation (e.g. sunlight) which contains blue light, making it impossible to disentangle its effects from those of blue light.

Plants acclimate to their environment by adjusting their morphology, among other traits. Blue light supplementation typically suppresses shoot elongation and leaf expansion (Gaba et al., 1984; Ahmad, 2002; Hernández and Kubota, 2016; Kaiser et al., 2019), thereby reducing whole-plant light interception. Similarly, plants exposed to UVB radiation consistently exhibit a compact phenotype (Neugart and Schreiner, 2018). For UVA radiation, on the other hand, we have previously found that added to red and blue light, it significantly stimulated plant height and leaf growth in tomato and lettuce (Kang et al., 2018; Chen et al., 2019). Such UVA properties are beneficial for light capture and consequently resulted in higher biomass production. Similarly, Jansen and Biswas (2012) reported that UVA radiation substantially increased (by 30 %–150 %) rosette diameter in eight natural accessions of *Arabidopsis thaliana*. It thus seems that UVA radiation has different effects on plant morphology than either blue or UVB. Leaf angle and leaf length/width ratio are properties of plant architecture that affect light interception (Sarlikioti et al., 2011). Steeper leaf angles often allow more light to penetrate to leaves lower in the canopy, which may be beneficial for whole-plant light absorption (Falster and Westoby, 2003). On the other hand, plant architecture is strongly regulated by the light environment (Pearcy et al., 2005; van Zanten et al., 2010). Keller et al. (2011) suggested that blue light attenuation is an important control of shade avoidance syndrome (SAS) in *Arabidopsis thaliana* that is characterized by leaf hyponasty and reduced lamina/petiole ratio, and these morphological responses are suggested to be correlated with the brassinosteroid signal pathway. Auxin is involved in the blue light signaling pathway, and it can move from the illuminated to the shaded side of plants and becomes asymmetrically distributed to regulate leaf position (Esmon et al., 2005). However, to date we do not know how plant architecture changes in response to UVA radiation and which consequences this has for plant growth.

Leaves of plants grown under red light alone are often characterized by dysfunctional photosynthesis, which can be observed as e.g. low photosynthetic capacity, reduced photosynthetic electron transport, and unresponsive stomata (Matsuda et al., 2004; Hogewoning et al., 2010). These symptoms are commonly referred to as the ‘red light syndrome’, and they might be caused by a disrupted leaf ultrastructure, malfunctioning PSII components and excess nutrient accumulation under pure red light (Chang et al., 2016; Miao et al., 2019). Under monochromatic red light, activation of cryptochromes and phototropins does not take place, leading to a suppression of expression of genes encoding several chloroplast and PSII components (Walters, 2005). Indeed, the blue/UVA photosensory pathway has been shown to be involved in the maintenance of PSII core protein synthesis (Christopher and Mullet, 1994; Mochizuki et al., 2004). Hogewoning et al. (2010) suggested that in cucumber, at least 7% of blue light during growth is required for normal photosynthetic functioning; also, the ‘red light syndrome’ can be reversed by blue light (Trouwborst et al., 2016). UVA radiation has been reported to efficiently induce cryptochrome and

phototropin based signaling (Christie et al., 2015). This raises the question of whether and to what extent UVA radiation, instead of blue, could reverse the ‘red light syndrome’.

UV radiation induces the formation of leaf phytochemical components, in particular of phenolics and flavonoids (Neugart and Schreiner, 2018). Adding UVA to visible radiation significantly stimulated phenolic compound accumulation in various species grown in controlled environments (Maffei et al., 1999; Lee et al., 2014a, b; Moreira-Rodriguez et al., 2017). In field attenuation experiments, the exclusion of UVB resulted in a decrease in total phenolic compounds, and excluding both UVB and UVA magnified such drops in individual phenolic compounds (Kotilainen et al., 2009; Morales et al., 2010). Blue light also plays a key role for phytochemical production (Holopainen et al., 2018; Liu et al., 2018a). Siipola et al. (2015) reported that solar blue light instead of solar UV radiation can be the main regulator of phenolic compound accumulation for pea plants (*Pisum sativum*) grown outdoors. In this context, the function of UVA and blue light on regulating secondary metabolism needs to be further clarified.

This study aimed at exploring how UVA radiation affects plant morphology and physiology, and at distinguishing to what extent these effects differ from those of blue light. Tomato plants were grown under monochromatic red light, dichromatic red and blue light, as well as dichromatic red light and UVA radiation (with two doses of UVA), all treatments containing identical photon flux density (PFD). Plant growth, morphology and leaf physiology was characterized.

2. Material and methods

2.1. Plant material and growth conditions

Tomato seeds (*Solanum lycopersicum*, c.v. ‘Moneymaker’) were germinated in rockwool plugs (Grodan, Roermond, the Netherlands) under 100 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ white LED light, and transferred to rockwool cubes (10 cm \times 10 cm \times 7 cm; Grodan) upon unfolding of the second true leaf for treatments in a growth room. CO₂ partial pressure was close to ambient, day/night temperature was 23/21°C, and relative humidity was 65–70 %. Photoperiod was 16 h. Plants were regularly irrigated with modified Hoagland nutrient solution (pH = 5.5; EC = 2.0 dS·m⁻¹).

In the growth room, two cultivation frames were fixed, and each frame was divided into three layers (6 cultivation units in total). Dimensions of each frame were: 130 cm length \times 70 cm width \times 210 cm height. The upper four cultivation units were used in this study. To avoid light contamination, opaque black-white plastic films were wrapped around each cultivation unit with the white side facing the plants. Two ventilation fans (12 V, 0.90 A) were installed in each unit to ensure uniform air circulation. LED light tubes (iGrowLite Co. Ltd, Guangzhou, China), of which PFD can be controlled, were mounted in each cultivation unit 70 cm above the growth plate. PFD, measured 25 cm above the growth plate, was 250 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, and was provided by monochromatic red light (R), a mixture of red and blue (R + B), or mixtures of red and UVA radiation (R + UVA; Table 1). Peak intensities of UVA, B and R were 370, 450 and 660 nm, respectively (Fig. 1). Light intensity and spectra were routinely monitored using a spectroradiometer (Avaspec-2048CL, Avates, Apeldoorn, The Netherlands).

Table 1
Details of the experimental light setup.

Treatments	Red ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	Blue ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	UVA ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	Total incident PFD ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)
R	250	\		250
R + B	215	35	\	250
R + UVA(L)	234	\	16	250
R + UVA(H)	215	\	35	250

R, monochromatic red light; R + B, mixture of red and blue; R + UVA(L), mixture of red and low intensity of UVA; R + UVA(H), mixture of red and high intensity of UVA; Peak intensities of UVA, B and R were 370, 450 and 660 nm, respectively.

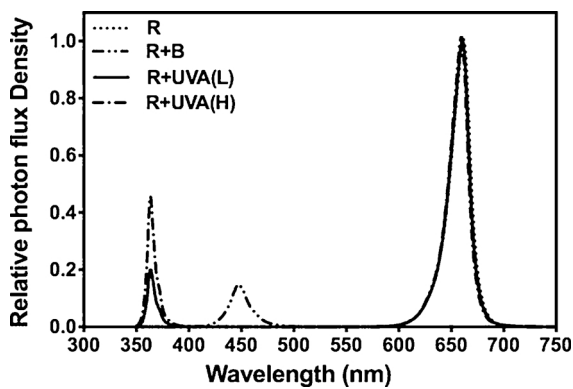


Fig. 1. Relative photon flux density of the four treatments: monochromatic red light (R), mixture of red and blue (R + B), mixture of red and UVA with low (L) and high (H) intensities. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Four batches of plants were successively grown in each treatment (eight plants were grown per treatment and batch). Plants were rotated daily in a random fashion to avoid position effects on plant growth. The treatment position in the growth room was randomly switched whenever new cultivation started. These plants were used for plant growth and morphological analysis, as well as for measurements of leaf photosynthesis and biochemical components.

To determine hormone concentrations under the various treatments, a transfer experiment was conducted: plants were firstly grown under monochromatic red light for two weeks, after which they were divided into three groups and distributed to R, R + B, and R + UVA (H) treatments, respectively, for another week. Growth conditions were identical to those described above.

2.2. Plant growth and morphology

Destructive measurements were carried out 21 days after the start of treatments. Four plants per treatment were harvested in the first batch of plants, and seven plants per treatment were harvested in the second and third batches of plants, respectively, resulting in a total of 18 harvested plants per treatment. Fresh and dry weight of leaves, lateral buds and stems was determined. Plant organs were dried for 72 h at 80 °C in a ventilated oven (DHG-9070A, Shanghai Jinghong, Shanghai, China). Leaf area was measured with a leaf area meter (LI-3100C, Li-Cor Biosciences, Lincoln, Nebraska, USA). Specific leaf area (SLA) was calculated by dividing leaf area by leaf dry weight. Stem length, leaf length and width were measured with a ruler. Leaf length and width were measured on the widest point of the 3rd, 4th, and 5th leaves. All mentions of leaf numbers herein refer to counting from the bottom of the plants.

In the fourth batch of cultivation, plants were treated for ten days, and eight plants per treatment were used for measurements of leaf morphology. At the 6th and 10th days of treatments, images were taken from the side view (Fig. S1), which showed the leaf angle distribution of the 1st and 2nd true leaves at day six, and that of the 2nd and 3rd true leaves at day ten. These images were used to quantify the leaf angle, defined as the angle of the tangent line to the leaf petiole with the vertical plane (90°; Inoue et al., 2008) by Image J (version 1.52a; <https://imagej.nih.gov/ij/>). Images were also taken from the top view of plants, which showed the projected plant area at day six (Fig. S2) and day ten (Fig. S3). These images were used to quantify whole-plant projected leaf area by comparing pixel numbers of the projected range of the whole plant with the pixel numbers of a white card (2 × 2 cm) using Adobe Photoshop CC (version 19.1.4) following Jarou (2009).

2.3. Leaf optical properties

In the third batch of plants, per treatment four leaflets from leaf number four of different plants were randomly selected to determine leaf optical properties. Leaf reflectance (Rf) and transmittance (Tr) were measured with a spectroradiometer (Ocean Optics USB2000+, Dunedin, FL) in combination with two integrating spheres (Ocean Optics FOIS-1 and ISP-REF). Leaf absorbance (Ab) was calculated as: $Ab = 1 - (Rf + Tr)$.

2.4. Gas exchange and chlorophyll fluorescence

Gas exchange and chlorophyll fluorescence were measured in the first batch of plants, on day 12 and 13 after the start of treatments, between 8:30 and 16:30. Measurements were performed on the fourth leaf, using the LI-6400XT photosynthesis system (Li-Cor Biosciences) with the leaf chamber fluorometer (Li-Cor Part No. 6400-40, area 2 cm²), in which a mixture of red (90 %) and blue (10 %) LEDs with peak intensities of 635 and 465 nm, respectively, was provided. For determination of net photosynthesis rate (A) in response to photosynthetic photon flux density (PPFD), leaves were firstly adapted to the cuvette at 250 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PPFD until A and stomatal conductance (g_s) stabilized. Thereafter, leaves were exposed to 250, 150, 50, 0, 400, 600, 900, 1200, 1500, and 1800 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PPFD. At each PPFD, measurements were taken when A had stabilized (~10 min/PPFD step). The data were fitted to a non-rectangular hyperbola model (Thornley, 1976), through which maximum photosynthesis rate at saturating light (A_{max}), light-limited quantum yield for CO₂ fixation (α), and dark respiration (R_d) were estimated. During measurements, CO₂ partial pressure was 450 $\mu\text{mol}\cdot\text{mol}^{-1}$, leaf temperature was 22 °C, leaf-to-air vapor pressure deficit ($\text{VPD}_{\text{leaf-air}}$) was maintained between 0.7–1.0 kPa, and the flow rate of air through the system was 500 $\mu\text{mol}\cdot\text{s}^{-1}$. Measurements were taken on four plants per treatment. During gas exchange measurements, chlorophyll fluorescence parameters (F_m' , maximum fluorescence yield of a light-adapted leaf; F_s , fluorescence under actinic light; and F_o' , minimum fluorescence yield of a light-adapted leaf) were recorded simultaneously. Maximum and minimum fluorescence yields of dark-adapted leaves (F_m and F_o , respectively) were measured in leaves that had been dark-adapted overnight. Photochemical quenching (qP), non-photochemical quenching (NPQ) and maximum photosystem II (PSII) efficiency (F_v/F_m) were calculated following Baker (2008).

2.5. Leaf biochemical components

2.5.1. Pigments

Leaf discs (1 cm²) from the third and fourth leaf were collected and stored in 10 mL 95 % ethanol in the dark at 4 °C for 48 h. The absorbance of the extract was measured at 665, 649 and 470 nm using a UV-vis spectrophotometer (UV-1800, Shimadzu, Japan). Chlorophyll concentrations were calculated using the equations derived by Lichtenthaler and Buschmann (2001).

2.5.2. Nitrogen

Dry leaf samples were collected and ground using a grinder for determining leaf total nitrogen concentrations with an elemental analyser (vario PYRO cube, Isoprime, UK), according to Liu et al. (2015).

2.5.3. Carbohydrates

Frozen leaf samples (0.3 g) were homogenized in 8 mL 80 % ethanol using a pestle and mortar and incubated at 80 °C for 30 min. The homogenate was centrifuged for 10 min (16,000 × g, 25 °C), the supernatant was set aside and 2 mL 80 % ethanol was added to the pellet. The 2 mL homogenate was centrifuged for 10 min (16,000 × g, 25 °C) and the supernatant was merged with the previously obtained supernatant. Soluble sugar contents were assayed in the supernatant using a

Table 2Plant growth traits in response to the four different light spectra treatments. Means \pm s.e ($n = 18$).

Treatments	Shoot dry weight (g·plant ⁻¹)	Dry matter content (%)	Dry mass partitioning to leaf (%)	Dry mass partitioning to stem (%)
R	6.5 \pm 0.3 b	8.4 \pm 0.2 b	74.8 \pm 0.6 b	17.5 \pm 0.5 a
R + B	6.9 \pm 0.3 ab	9.2 \pm 0.2 a	78.4 \pm 0.4 a	15.0 \pm 0.4 b
R + UVA(L)	7.7 \pm 0.2 a	9.1 \pm 0.2 a	76.9 \pm 0.5 ab	15.7 \pm 0.5 b
R + UVA(H)	7.6 \pm 0.3 a	9.1 \pm 0.2 a	75.8 \pm 0.6 ab	16.8 \pm 0.5 ab

Means followed by different letters within one column differ significantly ($P < 0.05$) as established by the least significant difference (l.s.d) test.

UV-vis spectrophotometer (UV-1800, Shimadzu, Japan) according to (Dubois et al., 1956). Starch content was quantified by adding 10 mL water to the pellets, and gelatinizing the mixture in a water bath at 100 °C for 60 min. Starch was enzymatically converted to glucose by thermostable α -amylase and amyloglucosidase at 55 °C, and then measured identically to soluble sugar contents.

2.5.4. Phenolics and flavonoids

Fresh leaf samples (0.1 g) were ground in liquid nitrogen using a mortar and pestle, then incubated with 1.5 mL 80 % aqueous methanol in an ultrasonic bath for 10 min, and centrifuged for 10 min (15,000 rpm, 4 °C). Total phenolic and flavonoid concentrations were determined by using the Folin-Ciocalteu and the aluminum chloride colorimetric assays, respectively (Marinova et al., 2005; Khanam et al., 2012). Absorbance against a prepared reagent blank was determined using a microplate reader (Infinite 200 PRO, TECAN, Switzerland). For total phenolics contents, gallic acid was used as the standard reference and GAE was expressed as mmol gallic acid equivalent (GAE)/100 g fresh mass (FW). For total flavonoid contents, rutin was used as the standard reference and RUE was expressed as mmol rutin equivalent (RUE)/100 g fresh mass (FW).

2.5.5. UV-absorbing compounds

Fresh leaf tissue (0.2 g) was ground in liquid nitrogen using a mortar and pestle, and then incubated with 5 mL of acidified methanol solution (70 % methanol, 29 % H₂O and 1% HCl) for 48 h at -20 °C. Absorbance of extracts was scanned in the 280–480 nm range using a microplate reader (Infinite 200 PRO, TECAN, Switzerland), and the concentration of UV-absorbing compounds was expressed as the absorbance OD·nm⁻¹ (Barnes et al., 2016).

2.6. Auxin (IAA) and brassinosteroid (BR) concentrations

One, two, and seven days after the transfer from red to other light treatments, four leaflets from the uppermost fully expanded leaf were flash-frozen and ground in liquid nitrogen and transferred to a freezer (-80 °C) for storage. Extraction and purification of IAA and BR were conducted following Bollmark et al. (1988) and He (1993), with modifications. Leaf tissue (0.5 g) was ground with 10 mL 80 % (v/v) methanol extraction medium containing 1 mM butylated hydroxytoluene as antioxidant in an ice-cooled mortar. The extract was incubated for 4 h at 4 °C and then centrifuged at 3500 g for 8 min at 4 °C. The supernatant was passed through Chromosep-C₁₈ columns (Sep-Park C₁₈ Cartridge, Waters, Milford, USA), which had been prewashed with 10 mL 100 % (w/v) and 5 mL 80 % (v/v) methanol, respectively. Hormone fractions were eluted with 10 mL 100 % (v/v) methanol and 10 mL ether from the columns, then dried by N₂ flow, and dissolved in 1 mL phosphate buffer saline (PBS) containing 0.1 % (v/v) Tween 20 and 0.1 % (w/v) gelatin (pH 7.5) for analysis. Mouse monoclonal antigens and antibodies against IAA and BR used in ELISA were produced at the Phytohormone Research Institute (College of Agronomy and Biotechnology, China Agricultural University, Beijing, China). The color in each well was detected using an ELISA Reader (model EL310, Bio-TEK, Winooski, VT) at an optical density of A₄₉₀. IAA and BR contents were calculated following Weiler et al. (1981).

2.7. Data analysis

The effects of UVA on plant morphological and physiological traits were evaluated by analysis of variance (ANOVA) with R 3.4.0. *Shapiro test* and *Bartlett test* were applied to test for normality and homogeneity of variance, after which a one-way ANOVA was performed. Subsequently, least significant differences (LSD) were determined to evaluate treatment effects at 95 % confidence level.

3. Results

3.1. Plant growth and morphology

UVA radiation promoted growth of tomato plants: Compared with monochromatic red light, shoot dry weight under both UVA treatments was significantly increased by 17–18 %, while the hybrid red and blue light treatment did not significantly increase shoot dry weight compared to pure red (Table 2). Dry matter contents in all three bichromatic treatments were significantly higher than those under monochromatic red light. There was a trend for more biomass to be partitioned to leaves and less to the stem under hybrid light compared to pure red light, but a significant difference was only detected between R and R + B treatments. The two UVA treatments did not differ from one another for these traits (Table 2).

Plants grown under different light quality treatments exhibited distinct morphological properties (Fig. 2). Leaf area in both UVA treatments was increased by 17–21 % compared to R, while R + B did not significantly increase leaf area compared to R (Fig. 3A). The tallest stems were observed under R, and the shortest in R + B, while stem length of both UVA treatments was in between those extremes (Fig. 3B). SLA of red light grown plants was significantly higher than that of all other treatments, indicating that plants under monochromatic red light formed thinner leaves (Fig. 3C). Leaves grown under both UVA treatments exhibited significantly lower leaf length/width ratios than those of the other treatments (Fig. 3D). Furthermore, leaves developed under pure red light were severely curled downwards and their lower petioles sloped downwards during growth, while these symptoms were strongly alleviated in the hybrid light treatments (Fig. 2). This was particularly obvious in both UVA treatments, which produced more even leaflets that were perpendicular to the light sources, resulting in a doubling of projected leaf area compared to R (89–106 %; Fig. 4A). Further, the R + B treatment resulted in a slight, but significant, increase in projected leaf area relative to R, but this was a lot lower than projected leaf area of both UVA treatments (Fig. 4A). Also, the UVA treatments resulted in smaller petiole angles (Fig. 4B) than R or R + B at days 6 and 10 during the light treatments. There was a UVA dosage effect on petiole angle, as that of R + UVA(H) was smaller than R + UVA(L) (Fig. 4B).

When plants that were first grown under pure red light were shifted to the other treatments, clear changes in plant morphology emerged after as little as two days, as leaves and petioles were visibly more upright in both blue and UVA treatments (Fig. 2, bottom panel). This clearly demonstrates that plants under UVA radiation are capable of quickly changing their relative leaf positions to intercept more light.

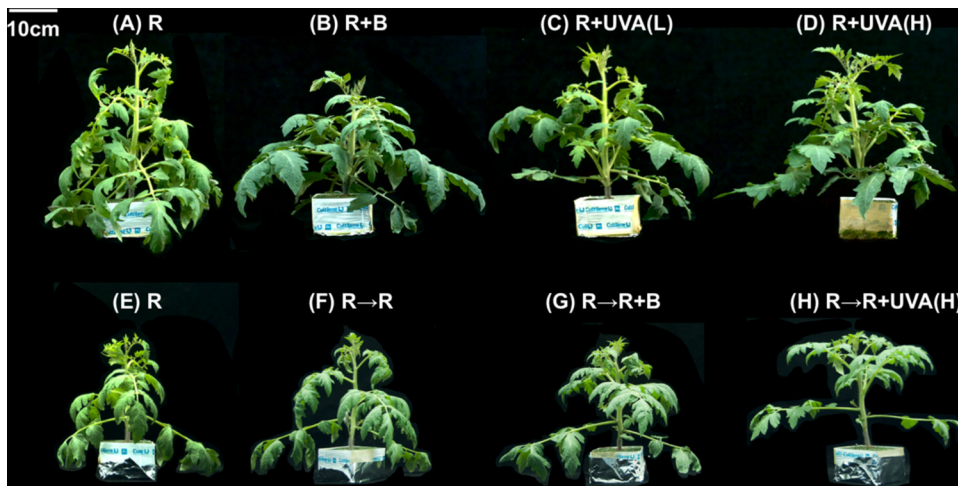


Fig. 2. Spectral treatment effects on plant morphology. Plants were grown under identical photon flux density ($250 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), which was provided by either monochromatic red light (R), or a mixture of red and blue (R + B), red and UVA with low (L) and high (H) intensities. Peak intensities of UVA, B and R were 370, 450 and 660 nm, respectively. The upper panel shows plants grown under R (A), R + B (B), R + UVA(L) (C) as well as R + UVA(H) (D) for 21 days; the lower panel shows tomato plants developed under R for 14 days (E) and then exposed to R (F), R + B (G), as well as R + UVA(H) (H) for two days. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.2. Leaf photosynthetic properties and leaf light absorption

Leaves that had developed under pure red light showed typical symptoms of the ‘red-light syndrome’: the irradiance response of photosynthesis was depressed compared with that of hybrid blue and red light treatments (Fig. 5A). Accordingly, A_{max} of these leaves was significantly lower than that of blue and red light treatments (Table 3). Adding UVA to red light eliminated this symptom, as leaf photosynthesis irradiance response curves and A_{max} were similar as those of the R + B treatment (Table 3). Average stomatal conductance was significantly lower in red light grown leaves at all PPFD levels compared to those under R + B, but not compared to both UVA treatments, in which g_s was intermediate (Fig. 5A, inset). Φ_{PSII} and qP showed similar trends as the photosynthesis irradiance response (Fig. 5B & D), while there were no clear treatment effects on F_v/F_m' (Fig. 5C) and NPQ (Fig. S4). R_d in both UVA treatments was significantly higher than that of red light treatments, while there was no significant difference between R and R + B treatments (Table 3). Photosynthetic quantum yield (α), F_v/F_m and leaf light absorption were unaffected (Table 3).

3.3. Leaf biochemical components

Leaves grown under red light had lower nitrogen, chlorophyll, carotenoid and carbohydrate contents than those grown under the

other treatments. There was no remarkable difference among the three hybrid light treatments, except that chlorophyll content in R + UVA (L) was slightly lower than under R + B. The chl a/b ratio was unaffected (Table 4).

Leaf secondary metabolites were also strongly affected by growth light quality: Leaves grown under R + B had significantly larger total phenolics and flavonoid contents compared to all other treatments, which did not differ from one another (Fig. 6A, B). The R + B treatment also triggered the strongest formation of UV-absorbing compounds, while pure R produced the fewest compounds and both UVA treatments were intermediate (Fig. 6C).

3.4. Auxin (IAA) and brassinosteroid (BR) contents

Red light grown plants, transferred to hybrid light treatments, showed significantly higher IAA and BR contents than those of plants consistently grown under red light, except for BR 7 days after transfer, which showed a similar value among treatments (Fig. 7). In fact, both IAA and BR contents became more similar between treatments as time progressed: At the 1st day after plant transfer, IAA content from the R + UVA (H) treatment was significantly higher than that of the R + B treatment, but this difference disappeared at the 2nd and 7th days after plant transfer to a treatment.

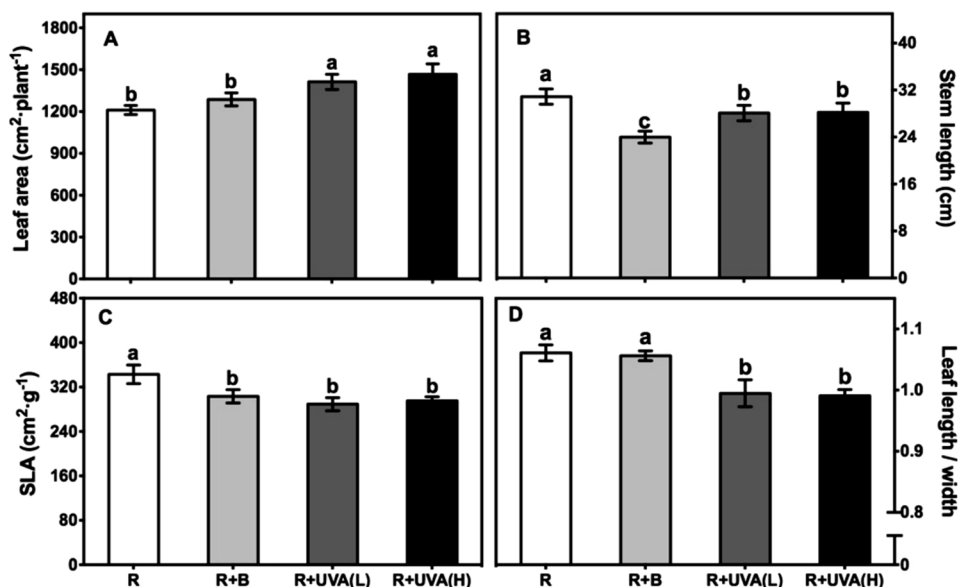


Fig. 3. Spectral treatment effects on leaf area (A), stem length (B), specific leaf area (SLA, C), and leaf length/width ratio (D) of tomato plants. Plants were grown under identical photon flux density ($250 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), which was provided by either monochromatic red light (R), or a mixture of red and blue (R + B), red and UVA with low (L) and high (H) intensities. Peak intensities of UVA, B and R were 370, 450 and 660 nm, respectively. Different letters show statistically significant differences between treatments ($P < 0.05$) as established by the l.s.d. test. Error bars show \pm s.e. ($n = 18$). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

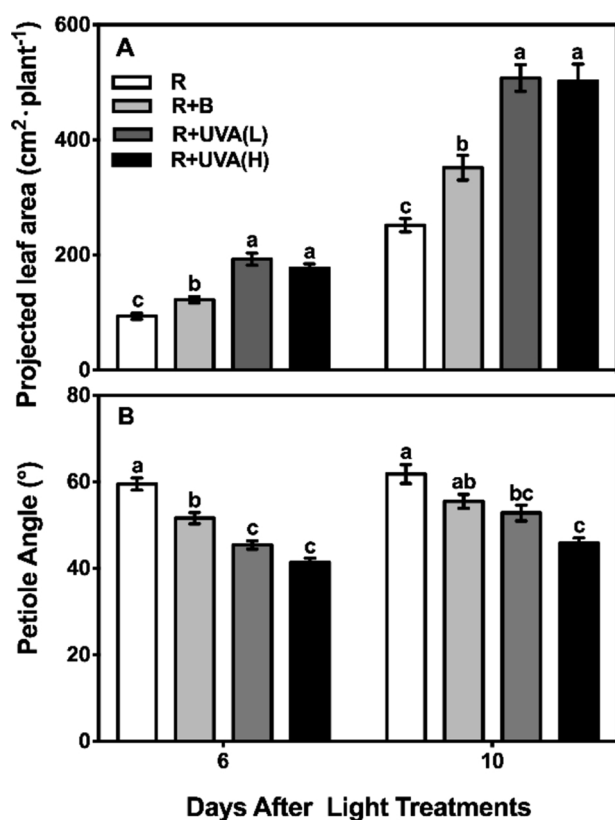


Fig. 4. Spectral treatment effects on projected leaf area per plant (A), and average petiole angle over first and second leaves (day 6) as well as second and third leaves (day 10), counted from the bottom of the plants (B). Plants were grown under identical photon flux density ($250 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$), which was provided by either monochromatic red light (R), or a mixture of red and blue (R + B), red and UVA with low (L) and high (H) intensities. Peak intensities of UVA, B and R were 370, 450 and 660 nm, respectively. Different letters show statistically significant differences between treatments ($P < 0.05$) as established by the l.s.d. test. Error bars show \pm s.e. ($n = 8$). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

Plant responses to UVA radiation have received substantial attention lately (Neugart and Schreiner, 2018; Kang et al., 2018; Lee et al., 2019; Mariz-Ponte et al., 2019; Chen et al., 2019). However, most insights regarding plant responses to UVA have been obtained using field attenuation experiments (Morales et al., 2010; Verdager et al., 2012; Zhang et al., 2014), or from controlled experiments in which UVA was supplemented to visible radiation that contains blue light (Jansen and Biswas, 2012; Lee et al., 2014a; Kang et al., 2018; Chen et al., 2019). These approaches make it difficult to fully take into account all the possible interactions with visible (PAR) and invisible (e.g. UVB) parts of the solar spectrum, and in particular with blue light, which shares photoreceptors with UVA radiation. Here, we eliminated these possible side effects and thereby disentangled UVA effects on several key physiological and morphological parameters from those of blue light.

4.1. UVA radiation affects leaf secondary metabolite accumulation less strongly than blue light

UV radiation is generally considered to induce antioxidant synthesis (Frohnmeier and Staiger, 2003; Neugart and Schreiner, 2018). Adding UVA to visible radiation has previously resulted in significantly higher antioxidant capacity, as indicated by increased total phenolic and flavonoid contents (Chen et al., 2019; Lee et al., 2019). Our study,

however, suggests that adding UVA to red light reduced flavonoid and phenolic contents (Fig. 6A & B), as well as UV-absorbing compounds (Fig. 6C), compared to leaves grown under treatments of R + B. This indicates that at least in tomato, UVA has a smaller effect on leaf secondary metabolite accumulation than blue. Blue light has been reported to be essential for synthesis and accumulation of diverse phenolic compounds (Son and Oh, 2013; Taulavuori et al., 2016). Siipola et al. (2015) reported that epidermal UVA absorbance compounds in leaves of *Pisum sativum* (mainly flavonoids) responded more strongly to blue than to UV radiation. This study as well as our current data are in agreement with Cominelli et al. (2008) who suggested that blue light stimulates the expression of genes related to flavonoid biosynthesis more strongly than does UVA.

Genes encoding chalcone synthase (CHS) have been considered as the first step in the flavonoid biosynthesis pathway (Kubasek et al., 1992; Liu et al., 2018b). CHS expression is regulated by light in a complex manner (Jenkins et al., 2001). In Arabidopsis, although the UVA/blue light induction of CHS expression involves the CRY1 photoreceptor (Wade et al., 2001), their phototransduction pathways responsible for flavonoid biosynthesis are distinct because UVA and blue light produce transient and relatively stable signals, respectively, and consequently may function differently in stimulating CHS expression (Fuglevand et al., 1996). Maximal CHS expression requires both blue and UV radiation (Fuglevand et al., 1996), which may explain UVA effects on secondary metabolite contents (in particular on flavonoids) shown in previous studies (Chen et al., 2019; Lee et al., 2019), all of which contained blue light next to UVA. Fuglevand et al. (1996) suggested that the combined effects of UVA and blue light are additive rather than synergistic. More work is needed to confirm this; also, concentrations of other secondary metabolites need to be determined to clarify the functions of UVA radiation in mediating secondary metabolite synthesis.

There is a consensus that fast plant growth is often associated with low levels of chemical defence as a trade-off strategy (Kurashige and Agrawal, 2005; Donaldson et al., 2006), because the induction of biosynthesis and accumulation of chemical components with a defence-promoting goal may be limited by substrate availability for growth (Treutter, 2006). From this point of view, the lower accumulation of foliar total phenolic and flavonoid contents under UVA treatments may contribute to greater plant growth, although this difference is not significant (Table 2), in comparison with the R + B treatment. However, it is still unclear to what extent UVA mediates the trade-off between plant growth and secondary metabolite formation.

4.2. UVA functions similarly as blue light in maintaining leaf photosynthetic functioning

Leaves developed under pure red light often show the 'red light syndrome', which is characterized by low photosynthetic capacity and unresponsive stomata, as observed in several previous (Hogewoning et al., 2010; Trouwborst et al., 2016; Zhang et al., 2018), as well as the current study (Fig. 5). The reduction in photosynthetic capacity correlates well with the reduction in total leaf nitrogen and chlorophyll contents under the red light treatment (Table 4). When measuring the light response of several chlorophyll *a* fluorescence parameters, there was a clear reduction in Φ_{PSII} and qP in pure red light grown leaves compared to those of other treatments, while F_v'/F_m' was unaffected (Fig. 5). Φ_{PSII} is product of F_v'/F_m' and qP , and our data suggest that the reduction in Φ_{PSII} was mainly attributed to the openness of PSII reaction centers (i.e., qP ; Baker, 2008) rather than NPQ, which was not strongly affected by the spectral treatments (Fig. S4), and typically correlates closely with F_v'/F_m' . These results are similar as those seen for cucumber (Trouwborst et al., 2016), and suggest that unlike the capacity for photosynthesis (e.g. A_{max}), the capacity for NPQ seems to be relatively less affected by the 'red light syndrome'. The underlying cause of the 'red light syndrome' is due to disorders in the development and

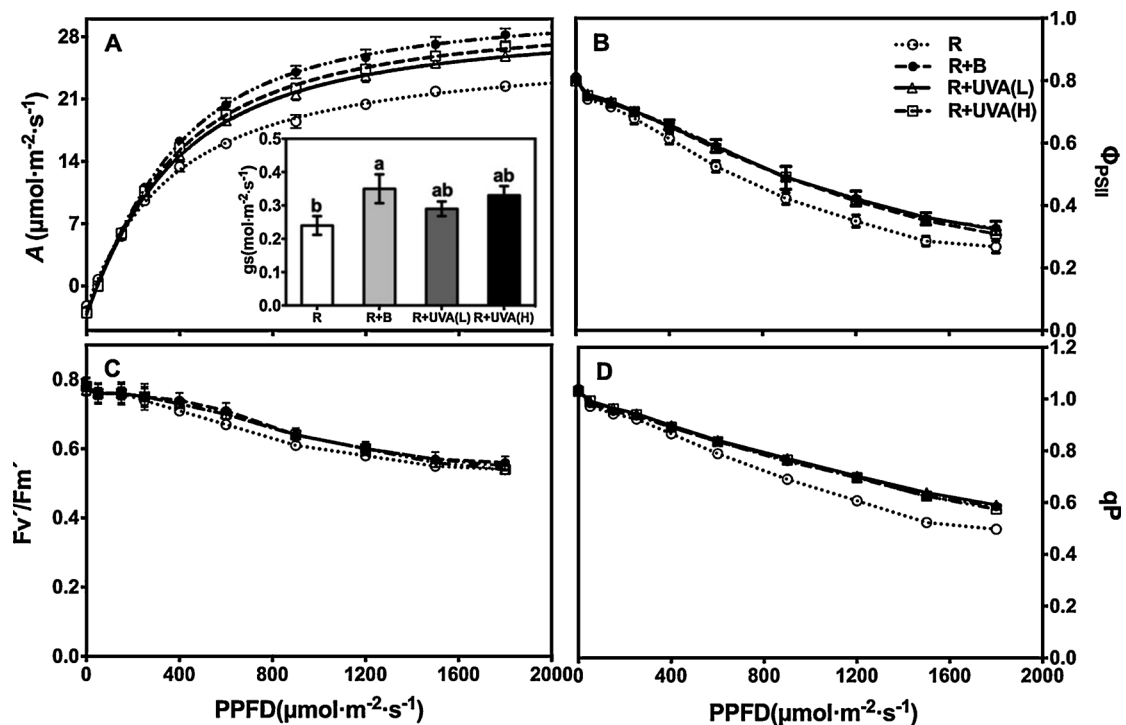


Fig. 5. Spectral treatment effects on the irradiance response of net photosynthesis rate (A; A), the PSII operating efficiency (B; Φ_{PSII}), photosystem II maximum efficiency (C; F_v/F_m) and photochemical quenching (D; qP). The inset in panel A shows average stomatal conductance (g_s) across all PPFD levels. Lines through data points of the irradiance response curves represent the fit to the non-rectangular hyperbola. Plants were grown under identical photon flux density ($250 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), which was provided by either monochromatic red light (R), or a mixture of red and blue (R + B), red and UVA with low (L) and high (H) intensities. Peak intensities of UVA, B and R were 370, 450 and 660 nm, respectively. Different letters show statistically significant differences between treatments ($P < 0.05$) as established by the l.s.d. test. Error bars show \pm s.e. ($n = 4$). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

functioning of the photosynthetic machinery (Chang et al., 2016; Miao et al., 2019). Hogewoning et al. (2010) concluded that blue light during growth is qualitatively required for normal photosynthetic functioning, and the symptoms of the 'red light syndrome' indeed were not apparent in the R + B treatment (Fig. 5, Table 3). Previous studies suggested that UVA/blue light photoreceptors (i.e. cryptochrome, phototropins) regulate the expression of chloroplast genes, which mediate overall transcription and expression of genes encoding PSII components, consequently maintaining a normal leaf photosynthetic development (Walters, 2005; Petroutsos et al., 2016). Therefore, it is not surprising that adding UVA to red light was similarly effective in eliminating the 'red light syndrome', as shown by a similar leaf photosynthetic capacities (Fig. 5, Table 3) and corresponding leaf biochemical contents, as those of blue light treatment (Table 4).

It is important to note that F_v/F_m in dark-adapted leaves was high (≥ 0.82) and unaffected by spectral treatments (Table 3), suggesting that pure red light in tomato did not seem to decrease the number of functional PSII reaction centers. This is interesting given that e.g. in cucumber, a relatively strong reduction in F_v/F_m was seen under red light (Hogewoning et al., 2010; Miao et al., 2019), and similar

reductions were seen in rapeseed (Chang et al., 2016). Therefore, compared to at least these species, the photosynthetic apparatus of tomato seems to be relatively less sensitive to the effects of abnormal development under monochromatic red light.

4.3. UVA promotes tomato growth through morphological adaptation leading to increased light interception

Plants integrate multiple light signals through photoreceptors to inform the processes leading to photomorphogenesis (Smith, 1982). UVA/blue light photoreceptors (i.e. cryptochromes, phototropins) participate in shaping plant morphology (Ahmad and Cashmore, 1993; Inoue et al., 2005; Christie et al., 2015). Also, blue light has unequivocally been shown to play a pivotal role for mediating leaf expansion, hypocotyl elongation, chloroplast accumulation and leaf movement (Inoue et al., 2005, 2008; Kang et al., 2008). Clearly, adding blue to red light can prevent the induction of abnormal plant morphology caused by pure red light, such as downward-facing leaves with curved leaflets (Fig. 2). Adding UVA to red light had similar effects to those of blue light, but with some distinctions (Fig. 2E, H): For example, increasing

Table 3

Leaf photosynthetic parameters and light absorption in response to the different light quality treatments. Means \pm s.e ($n = 4$).

Treatments	A_{\max}	α	R_d	F_v/F_m	Leaf light absorption (%)
R	29.3 ± 0.7 b	0.07 ± 0.001 a	2.36 ± 0.1 b	0.82 ± 0.003 a	91.96 ± 0.22 a
R + B	34.9 ± 1.0 a	0.07 ± 0.002 a	2.90 ± 0.3 ab	0.83 ± 0.002 a	93.14 ± 0.34 a
R + UVA(L)	33.5 ± 0.5 a	0.07 ± 0.002 a	3.19 ± 0.2 a	0.82 ± 0.001 a	92.49 ± 0.67 a
R + UVA(H)	34.5 ± 0.7 a	0.07 ± 0.003 a	3.23 ± 0.2 a	0.82 ± 0.002 a	92.52 ± 0.33 a

Means followed by different letters within one row differ significantly ($P < 0.05$) as established by the least significant difference (l.s.d) test.

Table 4
Leaf biochemical components in response to the different light quality treatments. Means \pm s.e (n = 11 for total nitrogen, chlorophyll and carotenoid content; n = 4 for carbohydrates).

Treatments	Total nitrogen (g·m ⁻²)	Chl a + b (mg·m ⁻²)	Chl a:b	Carotenoid (mg·m ⁻²)	End dark period		End photoperiod	
					Soluble sugar (mg·g ⁻¹ FW)	Starch (mg·g ⁻¹ FW)	Soluble sugar (mg·g ⁻¹ FW)	Starch (mg·g ⁻¹ FW)
R	1.7 \pm 0.1 b	268.4 \pm 4.4 c	3.5 \pm 0.02 a	42.9 \pm 0.4 b	8.9 \pm 0.2 b	47.0 \pm 6.1 b	13.9 \pm 2.0 b	140.7 \pm 28.7 b
R + B	1.9 \pm 0.1 a	369.4 \pm 6.8 a	3.4 \pm 0.03 a	55.3 \pm 1.1 a	11.4 \pm 0.6 b	70.7 \pm 9.0 a	19.5 \pm 1.9 a	186.3 \pm 20.6 a
R + UVA(L)	2.0 \pm 0.0 a	340.4 \pm 1.1 b	3.5 \pm 0.03 a	53.2 \pm 0.9 a	11.5 \pm 0.2 b	74.2 \pm 11.6 a	18.4 \pm 1.5 a	195.4 \pm 18.1 a
R + UVA(H)	1.9 \pm 0.1 a	353.4 \pm 6.7 ab	3.4 \pm 0.01 a	53.7 \pm 2.3 a	14.9 \pm 1.2 a	75.9 \pm 4.6 a	17.4 \pm 1.5 a	210.8 \pm 15.4 a

Means followed by different letters within one column differ significantly ($P < 0.05$) as established by the least significant difference (L.s.d) test.

blue light often reduces plant height and results in a compact plant canopy (Huché-Théliet et al., 2016), which is in line with our observations (Fig. 3A). However, replacing blue by UVA resulted in taller plants (17–18 %) and a larger leaf area (10–14 %), in comparison with blue light (Fig. 3A & B), which facilitated whole-plant light interception and consequently contributed to an increase in biomass (10–12 %; Table 2). This is in line with earlier studies in tomato and lettuce (Kang et al., 2018; Chen et al., 2019) as well as in kale (Lee et al., 2019). These studies cannot exclude potential synergistic effects between UVA and blue light. It has been suggested that blue light acting through CRY1 affects the expression of many genes, which suppresses stem growth by repressing gibberellin (GA) and auxin synthesis and/or sensitivity (Folta et al., 2003). In this context, it is possible that CRY1 is less sensitive to UVA than blue light, because the extent of stem growth retardation by blue light was greater than that of UVA (Fig. 3B). This possibility still awaits experimental verification, however.

Plants modulate leaf position or direction towards incoming radiation by detecting blue and UVA signals (Christie and Murphy, 2013; Christie et al., 2015). Replacing blue by UVA radiation resulted in steeper leaf angles, as shown by more upward petioles than those of blue light treated plants (5–20 %; Fig. 4B). Falster and Westoby (2003) showed that steeper leaf angles are beneficial for whole-plant light absorption, as they allow more light to penetrate to the lower leaves. Moreover, plants under UVA exhibited flatter leaves than plants under blue light (Fig. 2G & H), resulting in a larger difference in projected plant area (43–58 %; Fig. 4A) than the measured leaf area (10–14 %; Fig. 3A) between UVA and blue light treatments. These traits illustrate that plants under UVA used a larger proportion of their leaf area to intercept light than those grown under blue light (Figs. 2 & 4). In addition, downward-facing leaves of plants grown under pure red light quickly (within two days) remodeled their morphology after transfer to blue or UVA radiation (Fig. 2E–H); this change was more obvious under UVA than under blue light. This modulation of plant architecture may result from the higher foliar auxin and brassinosteroid contents, which increased within a day in UVA treated plants upon shifts from pure red light (Fig. 7). It has been reported that auxin synthesis and transport respond to blue light to activate cell wall expansion and rapid adjustment of leaf morphology and leaf position (Inoue et al., 2005, 2008). Previous studies have shown that blue/UVA absorbing cryptochromes play an important role in SAS under low blue light intensity (Franklin, 2016; Pedmale et al., 2016), and brassinosteroid responses are required for the full expression of the SAS phenotype under low blue light (Keller et al., 2011). Our data suggest that plants grown under UVA showed a tendency towards a SAS phenotype, as reflected by larger leaf area, steeper leaf angle and longer stems than under the blue light treatment (Fig. 3). Therefore, we speculate that UVA radiation may have similar functions as that of low blue light intensity on inducing SAS.

Plant growth largely depends on canopy light interception and daily light integrals (Li et al., 2014), unless plant growth is sink limited (Körner, 2015). We maintained similar PFD in all treatments (Table 1), also in the treatments containing UVA radiation. UVA has extremely low photosynthetic quantum yields (McCree, 1972), and can therefore be considered to be non-photosynthetic. This indicates that the effective photon flux density directly involved in leaf photosynthesis in both UVA treatments was lower than that of the other two treatments. Therefore, the larger biomass under both UVA treatments is very likely to be attributed to larger leaf area and plant architecture adaptation, both of which were beneficial for light interception, and happened despite a higher rate of dark respiration (Table 3), which most likely reduced diurnal carbon gain per unit of leaf area. It is evident that UVA stimulates the growth of young tomato plants, while it is unclear whether such a positive effect of UVA would happen during the fruiting stage plants, in particular for improving tomato fruit quality. Therefore, further study is needed to explore how UVA radiation affects greenhouse tomato.

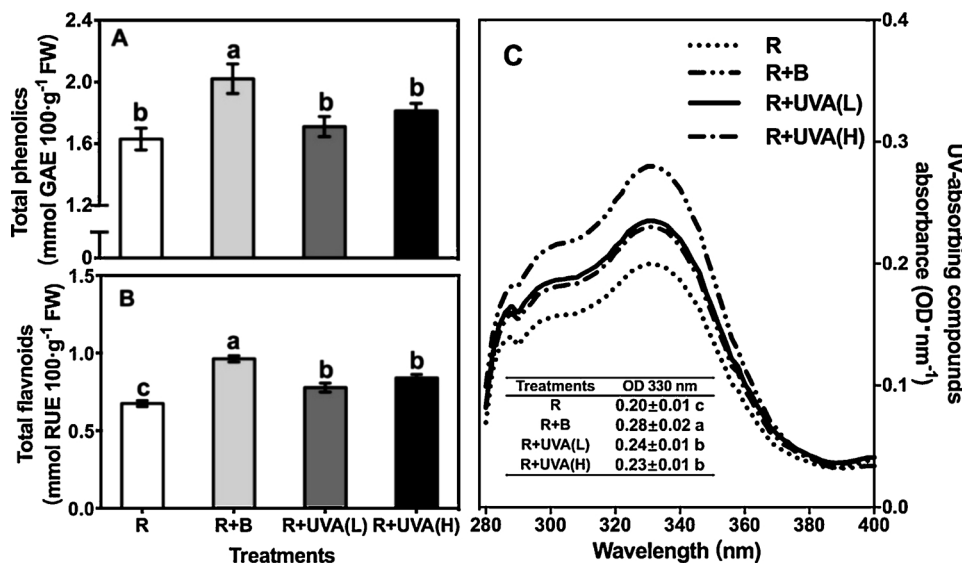


Fig. 6. Spectral treatment effects on total phenolics (A), flavonoids (B) and UV-absorbing compounds (C) of tomato leaves. The inset of panel C shows absorbance values of UVA-absorbing compounds, measured at wavelength 330 nm. Plants were grown under identical photon flux density ($250 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), which was provided by either monochromatic red light (R), or a mixture of red and blue (R + B), red and UVA with low (L) and high (H) intensities. Peak intensities of UVA, B and R were 370, 450 and 660 nm, respectively. Different letters show statistically significant differences between treatments ($P < 0.05$) as established by the l.s.d. test. Error bars show \pm s.e. ($n = 5$). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

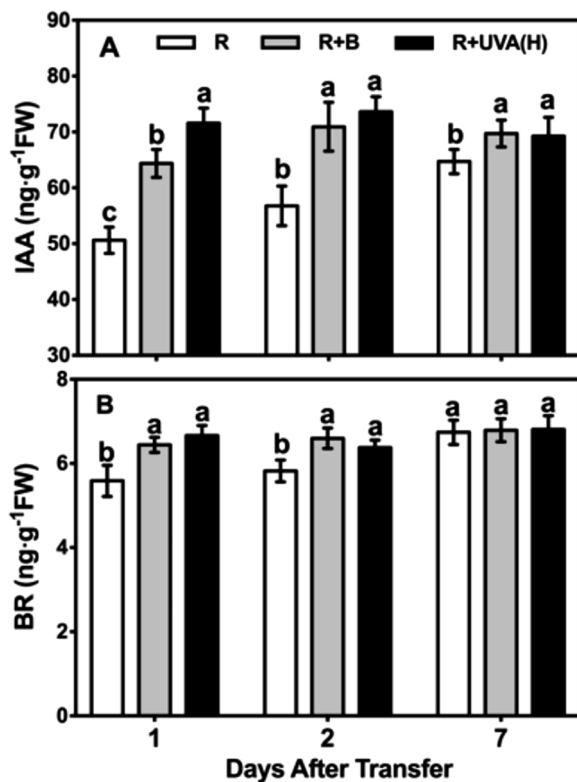


Fig. 7. Effects of a change in growth light spectrum on auxin (IAA) (A) and brassinosteroid (BR) (B) contents of tomato seedlings developed under red (R) for 14 days and exposed to a different spectrum for a period of 1, 2 and 7 days. Plants were grown under identical photon flux density ($250 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), which was provided by either monochromatic red light (R), or a mixture of red and blue (R + B), red and UVA with low (L) and high (H) intensities. Peak intensities of UVA, B and R were 370, 450 and 660 nm, respectively. Different letters show statistically significant differences between treatments ($P < 0.05$) as established by the l.s.d. test. Error bars show \pm s.d. ($n = 4$). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

5. Conclusions

Red and blue light are among the most important wavebands for leaf photosynthesis, and together are widely used in artificial light sources for plant growth. Replacing blue by UVA promotes tomato

growth through morphological adaptation leading to increased light interception, while it affects leaf secondary metabolite accumulation less strongly than blue light. Moreover, UVA functions similarly as blue in maintaining leaf photosynthetic functioning. Our result suggests that UVA cannot be unequivocally considered as an abiotic stress factor, and may provide the basis for future recipes for growing plants with artificial light.

Author statement

We would like to state that all authors have seen the revised version of the manuscript being submitted. They warrant that the article is the authors' original work, hasn't received prior publication and isn't under consideration for publication elsewhere.

Declaration of Competing Interest

The authors declare that they have no competing interests.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.envexpbot.2020.104073>.

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