



Supplementary UV-A and UV-B radiation differentially regulate morphology in *Ocimum basilicum*

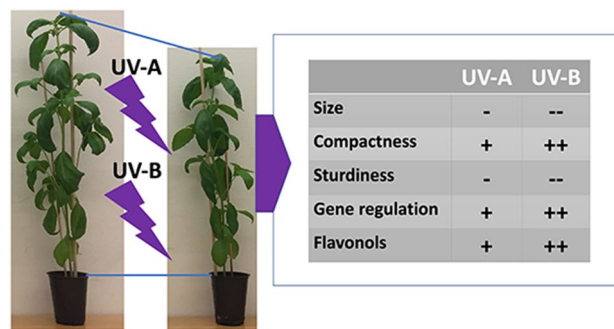
Minjie Qian^{1,2} · Irina Kalbina¹ · Eva Rosenqvist³ · Marcel A. K. Jansen⁴ · Åke Strid¹

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Abstract

UV-A- or UV-B-enriched growth light was given to basil plants at non-stress-inducing intensities. UV-A-enriched growth light gave rise to a sharp rise in the expression of *PAL* and *CHS* genes in leaves, an effect that rapidly declined after 1–2 days of exposure. On the other hand, leaves of plants grown in UV-B-enriched light had a more stable and long-lasting increase in the expression of these genes and also showed a stronger increase in leaf epidermal flavonol content. UV supplementation of growth light also led to shorter more compact plants with a stronger UV effect the younger the tissue. The effect was more prominent in plants grown under UV-B-enriched light than in those grown under UV-A. Parameters particularly affected were internode lengths, petiole lengths and stem stiffness. In fact, the bending angle of the 2nd internode was found to increase as much as 67% and 162% for plants grown in the UV-A- and UV-B-enriched treatments, respectively. The decreased stem stiffness was probably caused by both an observed smaller internode diameter and a lower specific stem weight, as well as a possible decline in lignin biosynthesis due to competition for precursors by the increased flavonoid biosynthesis. Overall, at the intensities used, UV-B wavelengths are stronger regulators of morphology, gene expression and flavonoid biosynthesis than UV-A wavelengths.

Graphical abstract



Keywords Flavonols · Gene expression · Morphology · UV-B · UV-A

1 Introduction

Plants as photosynthetic organisms are in their natural environment subjected to different wavelengths of the solar spectrum. Through different photoreceptor systems, plants use wavelengths from UV-B (280–315 nm) to far-red (> 700 nm) to regulate gene expression, metabolism and morphology [1]. With regards to UV, excessive exposure can be harmful

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to the organism, particularly due to the potential of UV-B to cause DNA damage [2] that in turn can lead to mutations and deleterious effects on plants' growth and development. From an evolutionary point of view, plants have evolved effective UV avoidance mechanisms, such as increased production of protective pigments to adapt to their environment [3].

Two signature plant responses toward low or moderate doses of supplementary UV are the accumulation of flavonoids in leaves [3] and alterations of plant morphology,

primarily in the form of increased compactness [4]. The flavonoid accumulation response is highly specific, with differences in flavonoid molecular composition, amounts and glycosylation pattern across species. In many species, flavonols are considered the main component of the UV response. These compounds can protect plants from UV light by either absorbing incoming UV photons or by scavenging reactive oxygen species (ROS) that are generated in UV-exposed plant tissue [3]. UV-induced flavonoid biosynthesis is characterized by increased transcription of genes encoding key enzymes of the phenylpropanoid and flavonoid biosynthetic pathways, such as phenylalanine ammonia-lyase (*PAL*), cinnamate-4-hydroxylase (*C4H*), and chalcone synthase (*CHS*) [3, 5]. However, compared with the large number of studies performed using UV-B light as the effector, our knowledge of UV-A as a regulator of plant development and metabolism is far from complete [6].

Morphological changes, such as decreases in leaf area, increases in leaf thickness, as well as shorter internode and petiole lengths, have often been observed in UV-exposed plants [4, 7, 8]. With regard to the function of these morphological changes, it has been argued that they minimize plants' exposure to UV and/or increase reflection [4]. Whether this is an avoidance strategy or not remains unclear since evidence for such an evolutionary development is lacking at present. Understanding the regulatory effects of UV wavelengths on plant morphology, metabolism and molecular biology is an important aspect of plant biology [9]. Whereas UV-B generally has an inhibitory effect on the development of plants and their organs, the same is not necessarily the case for UV-A (as reviewed by Verdager et al. [6]). For instance, UV-A can have stimulatory effects on *Arabidopsis* growth [10], implying the possibility of different regulatory pathways for the two types of radiation.

This type of knowledge also has applications in horticulture with regards to achieving plant phenotypes that are useful from a commercial perspective in the form of robust and easily transportable ornamental plants and/or that produce secondary metabolites that are favorable for human health. Many previous studies on UV regulation of plant physiology have been carried out on model species such as *Arabidopsis thaliana* [11], tree species such as birch (*Betula* spp.) [12], and with horticultural species such as tomato (*Solanum lycopersicum*) [13, 14], basil (*Ocimum basilicum*) [15, 16], and cucumber (*Cucumis sativus*) [5, 8, 17–29]. However, while many previous studies on crops have considered just one or two aspects of plant UV-B responses, this study integrates morphological, photosynthetic and gene expression analysis across both UV-B and UV-A parts of the solar spectrum and considering plant developmental aspects, resulting in a more comprehensive insight that can directly inform horticultural studies (e.g. with regards to workers' safety, cost of illumination equipment, shelf life, and transport losses

of horticultural produce). This study uses a single crop species as a model, yet given the conserved character of many molecular, physiological and morphological plant responses, it is anticipated that the outcomes apply to a broad range of commercially important crops.

Here, we study the regulatory patterns of key phenylpropanoid and flavonoid biosynthesis genes (*PAL*, *C4H*, and *CHS*) in the herbal plant species basil exposed to two different UV wavebands. In parallel, the effects of the two UV light qualities on morphological parameters were analyzed. Basil is a species that is fascinating both from a basic scientific viewpoint due to its interesting secondary metabolism [30] and from the fact that it is commonly sold in potted form in supermarkets, whereby its transportability, shelf life and content of nutritious phytochemicals are important quality traits.

2 Materials and methods

2.1 Growth of plants and light conditions

Basil seeds (*O. basilicum* cv. Sweet Aroma II) were sown in a 0.25 L pot with 14–7–15 NPK fortified peat (SE Horto AB, Hammenhög, Sweden). Seedlings were grown in a greenhouse using Vialox NAV-T Super 4Y high-pressure sodium lamps (Osram, Johanneshov, Sweden) for 16 h per day centered around solar noon, at 150–200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetic active radiation (PAR) as measured 20 cm above the table (equaling 30–40 W m^{-2} between 400 and 700 nm). The day/night temperature was 25 °C/20 °C and the relative humidity was set to 80%. Watering was done by adding water to the tray underneath the pots when the tray itself was completely dry. As soon as the basil seedlings had fully developed cotyledons, a full nutrient solution used in commercial production (Svegro AB, Ekerö, Sweden) was used for watering.

For experiments focused on morphological responses, 14 days after sowing, when the basil seedlings had a 1st well-developed true leaf pair, UV exposure commenced. For flavonoid accumulation and gene expression experiments, 21 days after sowing, when the basil seedlings displayed the 2nd well-developing true leaf pair, UV exposure was started. The plants were then given either supplementary UV-A-enriched or UV-B-enriched irradiation for 4 h per day (centered around solar noon) in addition to the PAR described above. Controls were simultaneously exposed to PAR only (see below) in the same chamber as the corresponding UV-treated plants. The UV-A and UV-B exposures were carried out in separate greenhouse chambers and the treatments were alternated between the chambers when repeating the experiment [5, 29].

Open top, front, and backside boxes (OTFB boxes), covered with Perspex on the left and right sides, were used for

the different UV exposures. Each greenhouse compartment was equipped with up to six boxes, three being used for the UV treatments and three for the corresponding controls. Each OFTB box contained up to 48 plants per replicate. For the UV-A-enriched exposures, fluorescent broadband UVA-340 tubes (Q-Lab, Cleveland, OH, USA) were used, whereas for the UV-B-enriched exposures, fluorescent broadband UV-B tubes Philips TL40/12 UV (Eindhoven, The Netherlands) were employed. For the control OFTB boxes, UV-blocking Perspex was used to cover the top and all sides. For the UV-B-enriched experiment, 0.13-mm cellulose acetate (Nordbergs Tekniska AB, Vallentuna, Sweden) covered the top, front, and backside of the OFTB boxes with the purpose to remove any UV-C radiation emitted by the Philips TL40/12 tubes. For the UV-A-enriched experiment, the OFTB boxes were similar to the boxes used in the control experiment but without any filtering material on top. The spectral distribution of the light in the different treatments was measured using an OL756 double monochromator spectroradiometer (Optronic Laboratories, Orlando, FL, USA) 20 cm above the table. The details of doses were described by Qian et al. [5]. Briefly, UV-A-enriched radiation contained 3.6 W UV-A m⁻² and a 45.5 mW m⁻² plant-weighted UV-B (the latter calculated according to Thimijan et al. [31] and Yu and Björn [32]), giving a total of 52.6 kJ UV-A m⁻² day⁻¹ and plant-weighted UV-B of 0.6 kJ m⁻² day⁻¹ during the daily 4-h UV exposure. The UV-B-enriched irradiation had 0.34 W UV-A m⁻² and 83.4 mW m⁻² plant-weighted UV-B totaling 4.9 kJ UV-A m⁻² day⁻¹ and 1.23 kJ m⁻² day⁻¹ plant-weighted UV-B. Thus, the UV-A-enriched light contained approximately 80-fold more UV-A than UV-B, whereas the UV-B-enriched light contained approximately fourfold more UV-A than UV-B [5]. Thus, the UV-A/UV-B ratio is 20-fold higher under the broadband UV-A tubes compared with the broadband UV-B tubes. The UV-A in the UV-B-enriched light was almost exclusively of wavelengths below 350 nm, termed UV-A_{sw} by Rai et al. [33], with reference to the part of the UV-A spectrum that gives rise to a gene regulatory pattern similar to that of UV-B. UV-A-enriched light was of wavelengths both below and above 350 nm, i.e. UV-A_{sw+lw}. For comparison with the intensity of natural UV-B in outdoor conditions, the daily irradiation outside in Lund, Sweden, under clear skies on a summer's day is approximately 4.8 kJ m⁻² day⁻¹ of plant-weighted UV-B [32], i.e. fourfold higher than that used in this study.

2.2 Chlorophyll *a* fluorescence measurements

The maximum quantum efficiency of PSII photochemistry, F_v/F_m [34] was measured on the youngest, well-developed leaf pair of two plants per OFTB box at 2 h past solar noon at the end of each experiment. The leaves were dark-adapted

for 30 min using dark clips and measured using a Handy-PEA (Hansatech Instruments, King's Lynn, UK). The dark clip was placed on the middle part of the adaxial side of the leaf blade avoiding major veins. The saturating pulse intensity used was 3500 μmolm⁻² s⁻¹ PAR for five seconds.

2.3 Flavonol content measurements

Adaxial (upper) surface flavonol content of the second true leaf (on days 1–5 of UV exposure, and days 6–8 without UV) was measured using a DUALEX Scientific+ (Force-A, Orsay, France) flavonoid fluorescence measurement device at the end of UV exposure each day, i.e. 2 h past solar noon. For each of the two repeats, six leaves from three different plants per treatment were measured ($n = 12$).

2.4 Isolation of mRNA and qPCR

Plant tissue was harvested on days 1–8 at two hours past the solar noon. The leaves were ground in liquid nitrogen, and RNA was extracted (RNAeasy Plant Mini Kit, Qiagen). A total of 1 μg RNA of high purity (a 260/280 nm absorbance ratio above 2.0 and a 260/230 nm absorbance ratio of 1.8–2.0) was used to synthesize cDNA (Mastercycler gradient thermocycler, Eppendorf, Hamburg, Germany) using a Maxima First Strand cDNA Synthesis #K1612 (Thermo Fisher Scientific, Hågersten, Sweden). Reverse transcription was performed according to the instructions of the provider (10 min at 25 °C followed by 20 min at 65 °C, and the reaction was terminated by heating at 85 °C for 5 min). A 5.5 μL sample of 20-fold diluted cDNA was used as the template for qPCR analyses (Step One Plus Real-Time PCR System, Thermo Fisher Scientific). The qPCR mixture (15 μL) contained 7.5 μL of Applied Biosystems™ PowerUp™ SYBR™ Green Master Mix (Thermo Fisher), 1.0 μL of each primer (5 μM), and 5.5 μL of cDNA. Reaction conditions for all the studied genes were: 2 s, 95 °C, and 40 cycles of 3 s, 95 °C and 30 s, 60 °C. All the primers used are listed in Supplemental Table S1, and the results of all qPCR reactions were normalized using the Ct values corresponding to the *ACTIN2* gene [35, 36].

2.5 Morphological measurements

After 28 days of UV treatment, morphological parameters were measured. A ruler was used to measure the lengths of stems and petioles. The dry matter of shoots (separated into stems, petioles, and leaves) and roots was measured using a Precisa (Dietikon, Switzerland) calibrated digital balance (accuracy 0.001 g) following oven drying at 70 °C for 20 h. The leaf area was determined from digitized photographs using ImageJ (<https://imagej.nih.gov/ij/>). For each

experiment, six plants per treatment were measured, two from each of the three replicated treatment OTFB boxes and their corresponding controls.

For stem bending measurements, one end of a 5 cm segment of the 2nd internode was firmly placed in a clamp, while a 30 g weight was attached via a thread to the other end of the stem segment. The bending angle of the internode was measured using a protractor.

2.6 Statistical analysis

Statistical analysis was performed using SPSS 27.0 (SPSS, Chicago, IL, USA). The data on morphological parameters were further analyzed using error propagation where the standard deviations of the ratios between UV-treated and control experiments were approximated using Taylor linearization [37] as further described in Qian et al. [8]. All the data were subjected to paired *T* tests, and *p*-values < 0.05 were considered statistically significant. Different significance levels were marked as: **p* < 0.05; ***p* < 0.01; ****p* < 0.005; *****p* < 0.001.

3 Results and discussion

3.1 Chlorophyll fluorescence, F_v/F_m

To ascertain that the low-dose UV exposures did not lead to plant distress [38], the fluorescence parameter F_v/F_m , representing the maximum potential quantum efficiency of Photosystem II, was measured. A decreased F_v/F_m upon prolonged exposure to stressful conditions generally is indicative of a deleterious effect on the plants, i.e. a decreasing efficiency of photosynthesis [34]. All UV-treated and control plants in this study had a steady F_v/F_m at approximately 0.82 in all experiments (Supplemental Fig. S1), showing that no such stress had been inflicted that would compromise the plants' functional capacity. Thus, the results of the following experiments represent measurements of UV effects in healthy non-stressed plants and are therefore consistent with literature that reports that low doses of UV have a regulatory rather than stress-inducing effect [38].

3.2 Leaf epidermal flavonols and expression of *PAL* and *CHS* in plants exposed to UV-enriched light

Both UV-A-enriched and UV-B-enriched light induced flavonol accumulation in basil leaves (Fig. 1). For control samples, the DUALEX flavonol index was around 0.25–0.30 during the 8 days of experiment with a slightly decreasing trend as the plants aged. A similar trend has also been reported for *Arabidopsis thaliana* rosettes [39]. In plants grown in UV-B-enriched light leaf epidermal

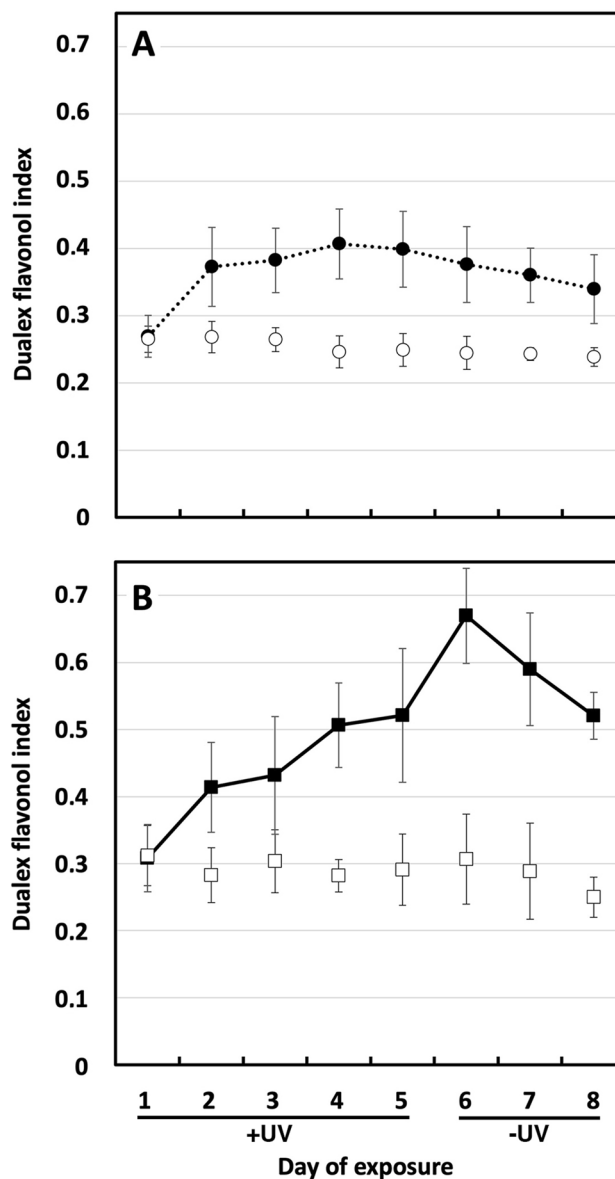


Fig. 1 Leaf epidermal flavonol content in basil plants exposed to UV. Basil plants that were 21 days old were exposed to either (A; circles) UV-A-enriched or (B; boxes) UV-B-enriched light for 5 days and were then left for 3 days in the corresponding PAR light only. Leaf epidermal flavonol content was measured using a DUALEX instrument at the end of UV exposure each day, 2 h past solar noon. Closed symbols represent UV-treated plants and open symbols represent the corresponding controls. The experiment was repeated twice and in each experiment 6 leaves from 3 plants of each treatment were measured, *n* = 12 and S.D. is indicated with whiskers. For the samples from days 2 to 8, the significance of the difference between the UV-exposed samples and their corresponding controls were all at the highest significance level: *****p* < 0.001

flavonol accumulation was significantly higher throughout the experiment (Fig. 1B) than in those plants grown under UV-A-enriched light (Fig. 1A). These data are consistent with reported less pronounced UV-A effects on flavonoid

accumulation, and even UV-A-mediated decreases in some experiments [6]. For all UV-treated plants, accumulation of flavonols was detected already on day 2 of the exposure (as measured at the end of UV exposure each day, i.e. 2 h past solar noon).

In plants grown in UV-A-enriched light, the flavonol levels peaked on day 4, with a Dualex index of 0.41. The flavonol level then decreased gradually after day 5 when UV exposure ceased. On the other hand, in plants grown in UV-B-enriched light, the peak was found on day 6, one day after cessation of exposure, at a Dualex index of 0.67, whereafter flavonol levels declined. The UV regulation of flavonol content in basil is in line with previous studies in a number of plant species, as reviewed for both UV-A [6] and UV-B [3]. This timeline is also consistent with many earlier reports, whereby the kinetics of flavonoid accumulation typically range in days [8, 40].

Expression of *PAL* (Fig. 2A), *CHS* (Fig. 2B), and *C4H* (Supplemental Fig. S2) genes was examined in basil over the 5-days UV exposure and 3-days recovery period after exposure of plants challenged with either UV light regime. The relative expression levels under UV-A- or UV-B-enriched light and their corresponding UV-less controls are normalized to the UV-A control = 1.0. Under UV-A-enriched light, the mRNA levels of the two phenylpropanoid biosynthesis genes (*PAL* and *C4H*) initially sharply rose, whereafter they dropped already during the UV exposure period. For plants exposed to UV-B-enriched light, the increased expression levels were found to be more stable over the exposure period. In both wavelength regions, induction of key biosynthesis genes precedes the accumulation of flavonols as measured by Dualex. Literature also reports that both UV-A and UV-B radiation induce transcript accumulation of *PAL* and *CHS* [6]. In fact, gene regulation by solar UV-A and UV-B radiation is complex and, in both cases, dependent on both the cryptochrome (CRY) UV-A photoreceptor and the UVR8 UV-B photoreceptor [33, 41].

For *PAL* and *C4H*, the transcript levels returned to control levels as soon as the UV exposure ended, i.e. up-regulation was between day 1 and day 5, the days of UV exposure. There was no difference between UV-treated and control samples from day 6 to day 8 when no supplementary UV was given. For *CHS*, the UV induction disappeared more slowly when UV supplementation was removed. Thus, there was still a higher *CHS* expression level at day 6 in plants exposed to UV-A-enriched light and on both day 6 and day 7 in plants exposed to UV-B-enriched light, compared with the corresponding control plants. In comparison, Dualex readings still show a clear difference in flavonol content between controls and, especially, UV-B treated plants several days following the cessation of the UV treatment, potentially indicating the long-lived character of flavonols.

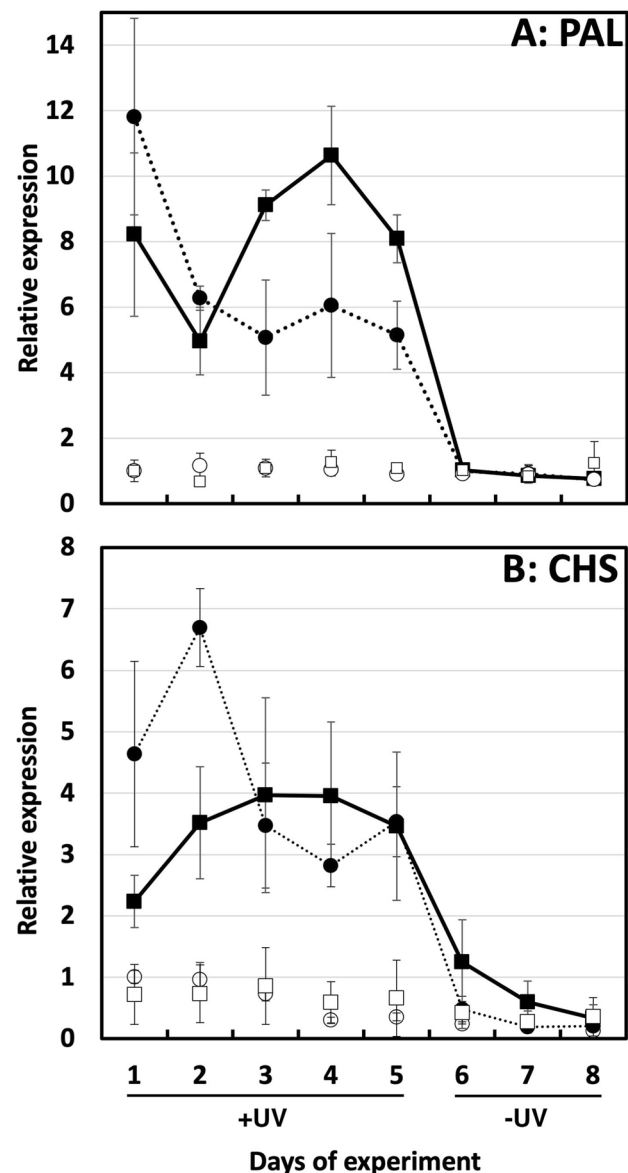


Fig. 2 Expression of the phenylpropanoid and flavonoid biosynthesis genes *PAL* (A), and *CHS* (B) expressed as the ratio between the expressions in exposed and control plants over 8 days, of which the five first contained a 4 h UV exposure centered around the solar noon, whereas during the last 3 days, the plants were exposed to PAR only. The symbols represent plants grown under UV-A (circles) and UV-B (boxes) enriched light. Closed symbols represent UV-treated plants and open symbols represent the corresponding controls. Relevant pairwise significances are given in Supplemental Tables S2 (*PAL*) and S3 (*CHS*). The data come from two different repeats of the experiment, with leaves from three different plants being analyzed in each, i.e. $n=6$

Thus, UV-A affects *PAL* and *CHS* expression more prominently the first few days, whereas UV-B gives a more stable *CHS* transcript level over the entire UV exposure period. Furthermore, plants grown in UV-B-enriched light retain a *CHS* expression higher than in control plants and also a few

days longer than in the UV-A-exposed plants. This is paralleled by the content of the epidermal flavonols (Fig. 1) that remains high in the plants grown in UV-B-enriched light throughout the experiment. The effect on *CHS* expression is probably related to the fact that the *CHS* enzyme is the first committed step of flavonoid biosynthesis, and thereby also of flavonols. As a signature response to UV-B, and due to the molecular function of flavonols, their biosynthesis has been shown to increase both UV-B screening and antioxidant capacity of plants [3, 42, 43]. After cessation of UV exposure there is less need for both UV screening and ROS scavenging and the flavonol levels slowly decline.

With regards to the expression of the individual members of the *PAL*, *C4H*, and *CHS* gene families, it was previously shown by Qian et al. [8] that UV-B-enriched light primarily up-regulated the *CsPAL4*, *CsC4H3*, and *CsCHS2* in cucumber leaves, whereas UV-A-enriched light mainly induced *CsPAL10*, and *CsCHS2*, implying further levels of differential regulatory effects of UV-A and UV-B light.

3.3 Morphology of basil plants grown in UV-enriched light

Upon qualitative visual inspection (Fig. 3), it was clear that exposure to both UV-A- and UV-B-enriched growth light led to shorter plants with shorter branches, i.e. more compact plants compared with the corresponding controls. This notion led us to further investigate in a quantitative way the effects of UV-enriched growth light on some morphological parameters of basil plants.

After 4 weeks of UV treatment, the stem length of plants treated with UV-A- or UV-B-enriched light was about 10% and 16% shorter, respectively, compared to PAR-only

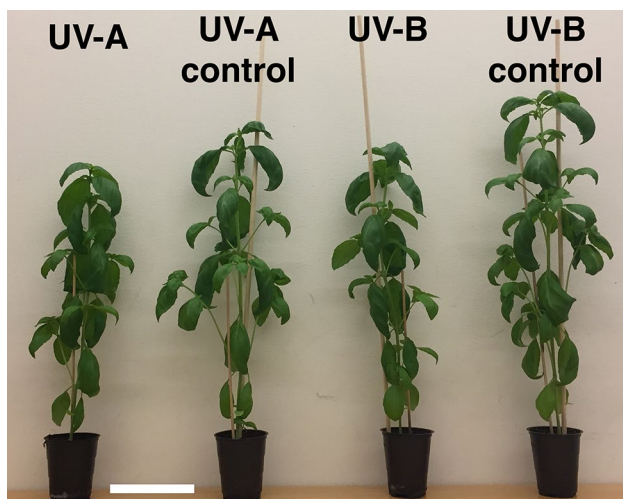


Fig. 3 Appearance of basil plants after 4 weeks of growth in UV-enriched light. The white bar represents 10 cm

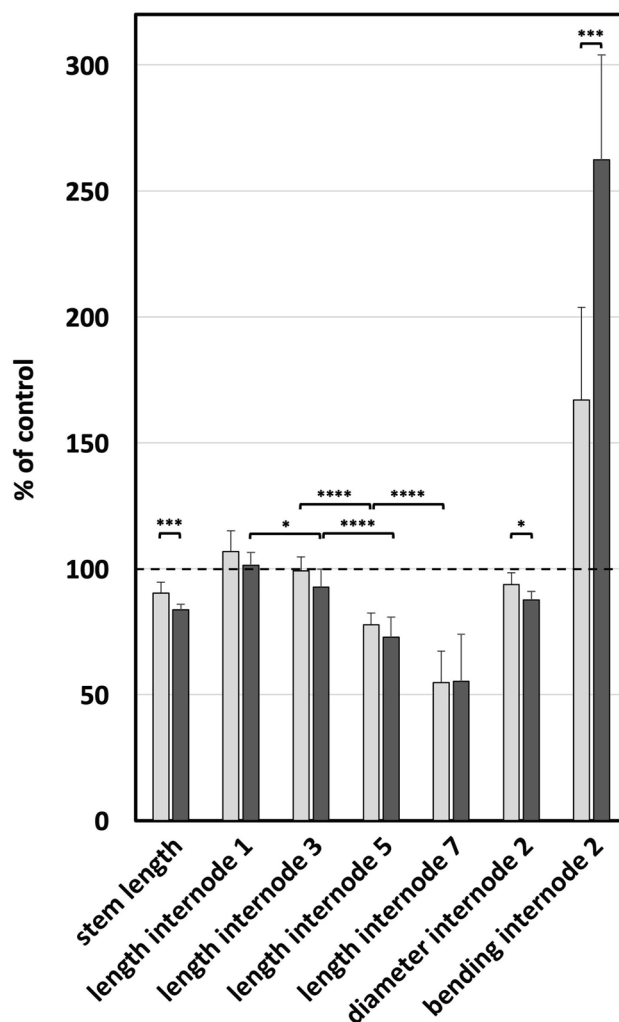


Fig. 4 The stem length, lengths of internodes 1, 3, 5 and 7, and diameter and bending of internode 2 as affected by UV-enriched growth light, compared with the same parameters under control light (= 100%). The UV-A-enriched treatment is represented by light grey bars and the UV-B-enriched treatment by dark grey bars. The bending angle was measured with a protractor after hanging a 30 g weight at the end of 5 cm internode segment while the other end was clamped to a tabletop. Some relevant pairwise significances are given (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.005$; **** $p < 0.001$) whereas the others are given in the Supplemental Table 4

controls (Fig. 4). This observation is consistent with the literature, in particular decreased stem elongation has been observed in a substantial number of studies (review by Robson et al. [4]). The UV-mediated inhibition of stem elongation was mainly due to the repression of the growth of young tissue. At present, the mechanism of this response is not fully understood, as both decreases in cell division as well as cell elongation have been reported [4]. Lack of stem elongation may relate to substantial changes in plant hormone metabolism, which in turn to some extent is related to photoreceptor activity [44]. For example, gibberellic acid, a

key hormone for stem elongation, is directly affected by UV radiation. For the plants grown in UV-A-enriched light, the inhibition of stem stretching was evident from the lengths of the 5th and 7th internodes, which were significantly shorter (Supplemental Table S4) by 22% and 45%, respectively, compared with control plants. The corresponding inhibition of stem elongation of plants grown in UV-B-enriched light could be observed by quantifying the lengths of the 3rd through to the 7th internode (Supplemental Table S4), where the lengths decreased by 7% (internode 3), 28% (internode 5), and 45% (internode 7), respectively (Fig. 4), compared with the controls. The effects of UV-A- and UV-B-enriched light on stem length in basil were qualitatively similar to the effects in cucumber [8]. In contrast, it has been shown in an outdoor study with *Sorghum bicolor* that UV-A exposure either can lead to increased or decreased stem length, compared with UV-less controls, in a cultivar-dependent fashion [45].

The internode diameter of the stem of basil plants was also significantly decreased (Supplemental Table S4) by growth in UV-enriched light (Fig. 4). As an example, the 2nd internode diameter decreased by 6% following the UV-A treatment and by 12% following the UV-B treatment. Strikingly, this change in lateral growth led to decreased stiffness of the stem, measured as the bending angle of the 2nd internode. This bending angle increased by 67% and 162% for plants grown in the UV-A- and UV-B-enriched treatments, respectively, highlighting a fundamental change in stem function inflicted by especially UV-B wavelengths (Fig. 4; Supplemental Table S4). The fact that *CHS* expression was up-regulated (Fig. 2) and flavonol levels were increased (Fig. 1) may have influenced stem stiffness by diverting phenylpropanoid precursors from lignin biosynthesis into flavonoids.

In this context, it is surprising that cucumber, which is a plant that generally is more sensitive to UV-induced morphological changes than basil [8, 29], became sturdier when grown in an identical UV-A-enriched light, as shown by a 21% decrease in the 2nd internode bending angle [29]. However, cucumber grown in UV-B-enriched light exhibited an increased bending angle by 183%, similar to the case with basil. This finding does again emphasize the fundamental difference between UV-A- and UV-B-mediated effects which, although sometimes similar, can in other cases be completely different [6].

It has previously been found in a study of cucumber [8] that petioles were particularly susceptible to growth retardation following exposure to UV-enriched light. UV-B-enriched light was a more efficient inhibitor of petiole growth than UV-A and the effect was more pronounced in younger tissues. For example, the 1st petiole was more than 10% shorter than the corresponding petiole in control plants, whereas petiole growth was retarded by more than 60% in

the 6th petiole [8]. Indeed, the UV mediated decrease in petiole elongation is one of the most commonly reported UV effects that has, for example, been noted in *Arabidopsis thaliana* as well as a host of other plant species [4]. Therefore, we were particularly interested to see whether a similar pattern was repeated in basil. Although both basil plants grown under both UV-A- and UV-B-enriched light had shorter petioles than the corresponding control plants, there was no consistent pattern with regards to either wavelength or tissue developmental age, although the trend was that, also in basil, younger tissue responded stronger to UV-treatment than older tissue (Fig. 5). The lengths of the 2nd, 4th, and 6th petiole of plants grown under UV-A-enriched light significantly decreased (Supplemental Table S5) by between 13 and 32% compared with their corresponding controls, whereas the petiole length of plants grown under UV-B-enriched light decreased (Supplemental Table S5) by between 18 and 29%. This finding complements the scarce literature on the comparison of UV-A and UV-B effects on petiole elongation [6], which appears to show consistent decreases in petiole elongation caused by UV-B, while UV-A has been reported to either increase

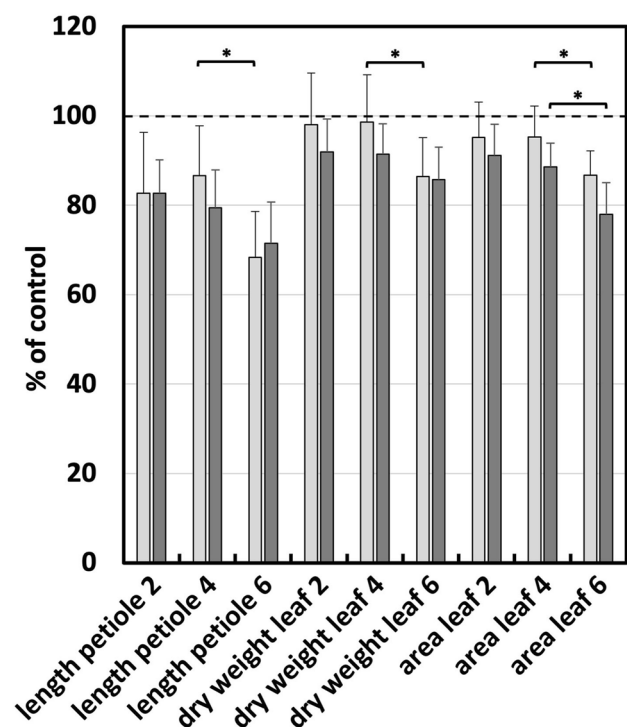


Fig. 5 The petiole length, the leaf dry weight, and leaf area of the 2nd, 4th, and 6th leaf as affected by UV-enriched growth light, compared with the same parameters under control light (=100%). The UV-A-enriched treatment is represented by light grey bars and the UV-B-enriched treatment by dark grey bars. Some relevant pairwise significances are given (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.005$; **** $p < 0.001$) whereas the others are given in the Supplemental Table 5

or decrease elongation. One possible explanation for the inconsistent UV-A effects is that the UV-A wavelength zone comprises two sub-zones, short and long UV-A wavelengths (315–350 nm, and 350–400 nm, respectively), which may interact differently with the various UV-photoreceptors [33].

The dry weight of leaf pairs 4 and 6 decreased (Supplemental Table S5) in basil plants grown under UV-B-enriched light (Fig. 5) with a larger decrease in the younger leaves (14%) compared to the older ones (9%). For plants grown in UV-A-enriched light, a statistically significant effect (Supplemental Table S5) was only seen for the 6th leaf pair where the decrease was 13% compared with the PAR control.

UV-B-enriched light also more efficiently inhibited leaf expansion than UV-A-enriched light. In the 2nd, 4th, and 6th true leaves, the leaf area significantly (Supplemental Table S5) decreased by 9, 11, and 22% (Fig. 5), respectively, in plants grown under UV-B-enriched light. Leaf expansion in UV-B-exposed plants has been studied in some detail, including the underlying effects on cell division and the cell cycle [46], as well as alterations in hormone metabolism [44]. A particularly notable change is the UV-B-induced change in auxin metabolism. For plants grown under UV-A-enriched light, there was a decreased leaf expansion only in the 6th leaf pair where the leaf area significantly decreased (Supplemental Table S5) by 14% compared with the control. Thus, once more, UV-A effects on morphological parameters are substantially less pronounced than UV-B effects [6].

In parallel with UV effects on stem, petiole and leaf development shown above, biomass accumulation of basil plants grown under UV-enriched growth light also decreased (Fig. 6; Supplemental Table S6). This is an interesting result given the lack of impact of either UV-A or UV-B enriched light on photochemical efficiency (Supplemental Fig. S1), and therefore most likely is related to the alteration in morphology. One possible scenario is that lack of petiole and leaf-blade elongation limits the capture of photosynthetic radiation resulting in a slowdown of photosynthesis at the whole plant level. Yet, this remains to be proven. Alternatively, UV-B-mediated stomatal closure [47] may also impede photosynthesis by impeding CO₂ intake. Consistent with the greater morphological effects of UV-B, UV-B-enriched growth light consistently inhibited biomass accumulation to a greater extent than UV-A-enriched growth light. The dry weight of stems and leaves proportionally decreased to a similar extent as the total plant weight, by 16, 16, and 15%, respectively, for plants grown under UV-A-enriched light, and by 28, 27, and 31%, respectively for plants grown under UV-B-enriched light. Unfortunately, however, there was a too large standard deviation in the measurements of the root dry weight (not shown) that did not allow us to draw any conclusion on the effects of UV-enriched growth light on root development in basil.

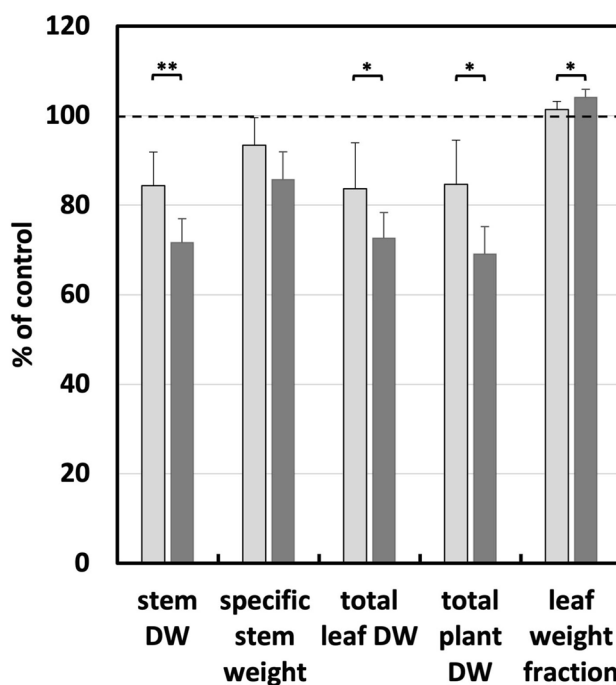


Fig. 6 The effect of UV-enriched growth light, compared with the same parameters under control light (=0%), on the biomass (dry weights) of different organs of basil plants grown under UV-enriched light. The UV-A-enriched treatment is represented by light grey bars and the UV-B-enriched treatment by dark grey bars. Some relevant pairwise significances are given (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.005$; **** $p < 0.001$) whereas the others are given in the Supplemental Table 4

Interestingly, as is seen in Fig. 6, the stem weight per unit length (specific stem weight) decreased (Supplemental Table S6) by 7% and 14% in plants grown in UV-A- and UV-B-enriched light, respectively, a fact that paralleled the observed decrease in internode diameter, as well as most likely stem stiffness (Fig. 4).

Finally, there was a small but significant (Supplemental Table S6) increase in the leaf weight fraction of 4% in plants grown in UV-B-enriched light (Fig. 6). UV-A had no effect on this parameter. Considering this limited effect on leaf weight fraction compared to other morphological parameters, this result indicates that overall stem morphology and overall growth is more affected by UV-enriched light than the internal allocation pattern between stem and leaves.

Our results indicate that younger tissue is more susceptible to UV, and particularly UV-B wavelengths than more mature tissue. This also is supported by a recent paper [8] where cucumber morphology was studied and young tissue was shown to be even more sensitive to growth light that was enriched in UV wavelengths. The greater vulnerability of the youngest tissue could possibly also be influenced by slightly higher UV levels at the top of the plant due to less

shading. However, UV light is well known to be particularly prone to scattering and reflection which thus leads to a higher influx into the canopy of this type of radiation from angles other than from above, compared with longer wavelengths of light [48]. Also, the difference in architecture of basil and cucumber plants is such that basil has a pair of leaves at each node, where cucumber only has one leaf. In the latter species, there is more space and possibility for light to penetrate the canopy and perhaps to increase the effect of UV to make cucumber more susceptible with regards to UV-induced inhibition of tissue development. However, just like in basil in the present study, there were no signs of stress in the cucumber plants grown either in UV-A- or UV-B-enriched light [8]. Also, although growth under UV-A- or UV-B-enriched light dwarfed cucumber plants, especially in those individuals that had been exposed to the UV-B wavelengths, the UV-induced dwarfing did not, in the end, lead to any significant effects on the fruit yield of these plants in a commercial greenhouse setting [8]. Intriguingly, whereas identical growth conditions led to sturdier cucumber plants under UV-A-enriched light [29], basil stem stiffness was negatively affected by both UV-A and UV-B treatments.

Another aspect of the lower susceptibility of basil to UV-induced growth inhibition may be the fact that basil grows in full sunlight in open spaces [49] and is thus adapted to a light environment with a considerable amount of UV in the normal growth light. Cucumber (*C. sativus*), on the other hand, is derived from wild ancestors, the present-day relative of which (*Cucumis hystrix*) has its habitat alongside streams on bushy hills approximately 1000 m over sea level with little direct sunlight and with high humidity [50, 51], and may therefore not have evolved to withstand considerable amounts of UV wavelengths. In addition, the cucumber elite clones used by Qian et al. [5, 8, 29] have been bred specifically for high harvest yields for commercial greenhouse production and may thus be even more susceptible than their wild ancestors to UV-induced regulation of tissue development.

4 Conclusions

Supplementing basil growth light with low, non-stress-inducing, irradiances of UV wavelengths led to the following:

- (i) increased levels of epidermal flavonols, UV-B-enriched light being a stronger inducer than UV-A-enriched light.
- (ii) a sharp rise in expression of the *PAL*, *C4H*, and *CHS* genes in basil leaves, an effect that rapidly declined after 1–2 days of exposure under UV-A-enriched light. UV-B-enriched light had a more stable and long-lasting effect on the expression of these genes.
- (iii) *CHS* gene expression remained up-regulated for at least two days after cessation of UV-B exposure.
- (iv) shorter more compact plants with a pronounced developmental effect in younger tissue relative to mature tissue.
- (v) a substantial decline in internode lengths, petiole lengths and stem stiffness. Decreased stiffness of the stem will render the plants less sturdy, and more prone to damage due to handling and transport. The stem stiffness was associated with observed decreases in internode diameter, lower specific stem weight and a possible decline in lignin biosynthesis.

Overall, UV-B wavelengths are a stronger morphological regulator than UV-A wavelengths.

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Data availability The datasets generated during the current study are available from the corresponding author on justified request.

Declarations

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this article.

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Authors and Affiliations

Minjie Qian^{1,2}  · Irina Kalbina¹  · Eva Rosenqvist³  · Marcel A. K. Jansen⁴  · Åke Strid¹ 

✉ Åke Strid
ake.strid@oru.se

¹ Örebro Life Science Center, School of Science and Technology, Örebro University, 70182 Örebro, Sweden

² School of Horticulture, Hainan University, Haikou 570228, China

³ Section of Crop Sciences, Department of Plant and Environmental Sciences, University of Copenhagen, Højbakkegaard Allé 9, 2630 Taastrup, Denmark

⁴ School of Biological, Earth and Environmental Sciences, Environmental Research Institute, University College Cork, North Mall, Cork T23 TK30, Ireland