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Different irradiances of UV and PAR in the same ratios alter the flavonoid profiles of *Arabidopsis thaliana* wild types and UV-signalling pathway mutants†

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The UVR8 photoreceptor in *Arabidopsis thaliana* is specific for ultraviolet-B (UV-B; 280–315 nm) radiation and its activation leads to a number of UV-B acclimation responses, including the accumulation of flavonoids. UVR8 participates in a signaling cascade involving COP1 and HY5 so that the absence of any of these components results in a reduction in the ability of a plant to accumulate flavonoids in response to UV; Cop1 mutants show high dropouts and *hy5-ks50 hyh* double mutants show very low levels of flavonoids. The predominant phenolics in *Arabidopsis thaliana* are sinapic acid derivatives as well as non-aclyated quercetin and kaempferol di- and triglycosides containing glucose and rhamnose as glycosylated sugar moieties. How this flavonoid profile in *Arabidopsis thaliana* is affected by UV radiation, how rapidly these changes occur in changing UV conditions, and which components of the UV-B signalling pathway are involved in rapid UV acclimatization reactions is poorly understood. In the present study, we examined these questions by characterizing the flavonoid profiles of *Arabidopsis thaliana* signalling mutants and wild types grown under different UV levels of constant UV-B+PAR ratios and then transferring a subset of plants to alternate UV conditions. Results indicate that flavonoid accumulation in *Arabidopsis thaliana* is triggered by UV and this response is amplified by higher levels of UV but not by all compounds to the same extent. The catechol structure in quercetin seems to be less important than the glycosylation pattern, *e.g.* having 2 rhamnose moieties in determining responsivity. At low UV+PAR intensities the introduction of UV leads to an initial tendency of increase of flavonoids in the wild types that was detected after 3 days. It took 7 days for these changes to be detected in plants grown under high UV+PAR intensities suggesting a priming of PAR. Thus, the flavonoid profile in *Arabidopsis thaliana* is altered over time following exposure to UV and PAR, but the functional significance of these changes is currently unclear.

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Introduction

Ultraviolet radiation (UV; 280–400 nm) accounts for a relatively small fraction of the total solar energy reaching the Earth's surface, but the radiation in this waveband is known to play an important role in regulating the growth and development of higher plants.[1,2] Highly energetic shorter wavelengths of solar UV (*i.e.*, terrestrial solar UV-B; 280–315 nm) can cause a number of deleterious effects in plants, including disruption of the integrity and function of important macromolecules (DNA, proteins and lipids), oxidative damage, partial inhibition of photosynthesis and growth reduction.[3–5] Plants have developed photosensory mechanisms to detect UV[6,7] and therefore protect and repair sensitive targets from direct and indirect UV-induced injury.[1,8] One of the most important and widespread protective responses of plants to UV radiation involves the induction and synthesis of flavonoids and related phenylpropanoid derivatives that function in UV screening and as antioxidants.[9–11]

UV-B-induced flavonoid biosynthesis appears to be mediated, at least in part, by the UV-B photoreceptor UV ResistanceLocus 8 [UVR8].[12,13] In *Arabidopsis thaliana*, UVR8 interacts with other elements of a signalling cascade including COP1 (the multifunctional E3 ubiquitin ligase Constitutively photomorphogenic 1), HY5 (Elongated Hypocotyl 5)[14] and HYH (Homolog of Elongated Hypocotyl) to control a number of UV-B acclimation responses.[15] After UV-B exposure, the UVR8 dimer is monomerized and accumulates in the nucleus.[12] COP1 is required for the nuclear accumulation of UVR8[16] and it stabilizes the bZIP transcription factor HY5. The release of HY5 results in the expression of genes involved in

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the biosynthesis of flavonoids and Repressor of UV-B photomorphogenesis (RUP1 and RUP2) that leads to the re-dimerization of UVR8.[12,16] In turn, the accumulation of flavonoids increases the plant's UV screening capacity and reactive oxygen species (ROS) antioxidant activity.[17]

Flavonoids are structurally diverse polyphenols that are ubiquitous in plants where they naturally occur as glycosides. The main flavonoids in *Arabidopsis thaliana* are quercetin and kaempferol glycosides that are not acylated.[18] While it is known that exposure to UV-B induces the biosynthesis of flavonoids and hydroxycinnamic acids,[19] which act in UV-shielding components and as antioxidants,[17] the specific composition and functional role of flavonoids can also be influenced by solar radiation regime. For example, shifting the flavonoid profile to polyhydroxylated flavonoids (*e.g.*, quercetin glycosides) in sun exposed, compared to shaded linden leaves, results in a higher singlet oxygen neutralizing capacity of sun-exposed leaves.[20] In kale, kaempferol glycosides show different antioxidant activities depending on their chemical structure.[21] Therefore, the response of flavonoid glycosides to UV-B depends on the chemical structure of the compound,[22–25] as well on the duration of UV-B exposure and the time of acclimation of the plant.[24,25] Glycosylation reduces the antioxidant activity of flavonoids and affects the accumulation, stability and solubility of flavonoids.[26,27] In broccoli, sinapic acid derivatives decrease at enhanced UV-B irradiation.[28,29] Remarkably, it has previously been shown that hydroxycinnamic acids act as scavengers of ROS induced by UV-B radiation.[30] The intracellular accumulation at sites of ROS production underlines the important antioxidant properties of the flavonoid.[31]

The accumulation of flavonoids and related UV-absorbing compounds in epidermal tissue decreases epidermal UV transmittance (TUV),[32,33] a mechanism by which plants acclimate to changing UV environments, including alterations resulting from stratospheric ozone depletion and climate change.[34,35] The ability of plants to accumulate these protective UV-absorbing compounds in response to days or weeks of exposure to UV is well known.[36] Recent studies have shown that many plants can also rapidly adapt their UV shielding (and total flavonoid level) in response to daily changes in solar UV-B and cloud cover shift.[37] However, which specific flavonoids contribute to these rapid changes in UV screening is not well understood. An interaction of UV and PAR has been shown in Arabidopsis.[38] Whether this is the influence of the ratio of UV to PAR or absolute intensities remains unclear.

In this study, we investigate how altered UV exposures affect the flavonoid profiles in wild type *Arabidopsis thaliana* and mutants lacking UV-B perception and signal transduction. Our goals are, (1) to assess the extent to which flavonoids, which differ in their chemical structure, are affected by specific components of the UV signalling pathway; (2) characterization of the variation of the flavonoid profile by UV irradiation during development and in response to rapid changes in UV radiation exposure; and (3) to evaluate how quickly plants can adapt their complete flavonoid profile to cope with rapid changes in UV exposure (*i.e.*, are certain compounds that respond more quickly to changes in UV exposure than others?).

Materials and methods

Experimental design

Wild types and UV-signalling mutants of *Arabidopsis thaliana*, which has been the model plant for the identification and isolation of the UV-B photoreceptor (UVR8) and UV-signalling pathways[39] were provided by Gareth Jenkins (University of Glasgow, UK). These included, Landsberg *erecta* (Ler) and its *uvr8-1* mutant, Columbia (Col-0) and its *cop1-4* mutant, and Wassilewskija (Ws) and its *hy5-ks50 hyh* double mutant. Seeds of all genotypes were sown in a peat-based substrate (Pro-Mix BX; Premier Tech Horticulture, Quakertown, PA, USA) and cold treated (+4 °C) for one week at which point they were placed in one of two temperature-controlled plant growth chambers at 159 μmol m^{-2} s^{-1} without UV irradiation for one week in order for cotyledons to emerge (EGC M12; Chagrin, OH. USA). These chambers were equipped with HID (high intensity discharge) bulbs (EYE MT400DL/BUD, Eye Lighting, Mentor, OH, USA) and two UV-emitting fluorescent bulbs (40 W UV-B-313; Q-Panel, Cleveland, OH, USA) that were each enclosed with clear cellulose diacetate film (JCS Industries, La Mirada, CA, USA) to eliminate UV wavelengths below *ca.* 290 nm. One chamber was arbitrarily assigned as a "low intensity" light regime chamber and the other a "high intensity" light regime chamber to study the effect of priming PAR on the effect of UV. Neutral-density shade cloth was placed below the HID lamps in the low- intensity chamber to reduce PAR at plant height from 542 μmol m^{-2} s^{-1} to 159 μmol m^{-2} s^{-1}. Similarly, the UV bulbs in the low-intensity chamber were wrapped with several layers of white cheese cloth to reduce effective UV-B irradiances from 252 mW m^{-2} (1.16 μmol m^{-2} s^{-1}) to 66 mW m^{-2} (0.30 μmol m^{-2} s^{-1}). We established these UV and PAR levels in the two chambers such that the ratios of UV-B : PAR were generally similar (UV-B : PAR expressed in units of mW m^{-2} : μmol m^{-2} s^{-1} were 0.42 and 0.46 in low- *vs.* high-intensity chambers, respectively). The irradiances of UV-A were 0.3 W m^{-2} (1.38 μmol m^{-2} s^{-1}) and 1.2 W m^{-2} (5.52 μmol m^{-2} s^{-1}) in the low- *vs.* high-intensity chambers, respectively. Each chamber was then given a "+ UV" and a "−UV" treatment by placing the plants under frames containing either UV-transparent film (Aclar type 22 A, 0.038 mm thick, Honeywell, Pottsville, PA, USA) or UV-blocking film (cut-off near 390 nm, CFC, 0.051 mm thick, LK Technologies, Maple Heights, OH, USA). Plants in the +UV treatment regime thus received both UV-B and UV-A radiation, whereas plants in the −UV treatment received no measurable UV-B or UV-A. Mean daytime and nighttime temperatures for both chambers were 23.6 °C and 18.7 °C, respectively, with a photoperiod of 10 hours.

UV spectral irradiance was measured with a double-monochromator UV/Vis spectroradiometer (Model OL 756, Optronic Laboratories, Orlando, FL, USA) and weighted according to a generalized plant action spectrum[40] normalized to unity at

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300 nm to obtain a measure of biologically effective UV irradiance (UV-B_{BE}). A broadband UV sensor (model SKU 430, Skye Instruments, Ltd., Powys, UK) was calibrated against this spectroradiometer and UV measurements were made periodically throughout the experiment with this sensor to verify UV treatment levels. PAR measured with a quantum sensor; model LI-185, Li-Cor, Inc., Lincoln, NE, USA.

Following emergence, seedlings were transferred to individual pots (one rosette per pot) and then grown for 3 weeks under either the +UV or −UV treatments in one of the two light regimes (*i.e.*, low- or high-intensity regimes). All plants were kept well watered throughout the experiment and were fertilized with an all-purpose plant food (Miracle Gro, OH, USA (NH_4 3.5%, NO_3 20.5%, P_2O_5 8%, K_2O 16%, B 0.02%, Cu 0.07%, Fe 0.15%, Mn 0.05%, Mo 0.0005%, Zn 0.05%)) weekly starting from week 3. At week 5 of the growth period, half of the plants in each UV treatment were transferred to the opposite side of the growth chamber (*i.e.*, the other UV treatment within the same chamber). Plants were harvested on day 3 and day 7 after this transfer. At the time of the harvest, digital photographs were taken of each plant to determine total plant leaf area and rosette width using Fiji imaging software.[41] Samples taken for flavonoid analysis were weighed to determine fresh mass; the samples were then frozen in liquid nitrogen, then freeze-dried (dry mass) and ground to a fine powder. The experiment was repeated three times independently with new sets of plants using the same plant growth chambers. A total of 192 plants were grown in each of the three independent trials with each trial consisting of 6 *Arabidopsis thaliana* genotypes under two intensities of UV and PAR, and four UV treatments (constant +UV exposure; switch from +UV to −UV; constant −UV exposure; switch from −UV to +UV). For the measurements of leaf area, fresh matter and dry matter and flavonoids, one plant was harvested per independent experiment.

Flavonoid analysis

Lyophilized *Arabidopsis thaliana* leaf tissue (0.01 g) was extracted in 600 µl of 60% aqueous methanol on a magnetic stirrer plate for 40 min at 20 °C.[42] The extract was centrifuged at 4500 rpm for 10 min at the same temperature, and the supernatant was collected in a reaction tube. This process was repeated twice with 300 µl of 60% aqueous methanol for 15 min each; the three supernatants obtained per sample were combined. The extract was subsequently evaporated until it was dry and was then suspended in 200 µl of 10% aqueous methanol. The extract was centrifuged at 3000 rpm for 5 min at 20 °C through a Corning® Costar® Spin-X® plastic centrifuge tube filter (Sigma Aldrich Chemical Co., St. Louis, MO, USA) for HPLC analysis.

Flavonoid identification (including hydroxycinnamic acid derivatives and glycosides of flavonols) and quantification was made using a series 1100 HPLC chromatograph (Agilent Technologies, Waldbronn, Germany) equipped with a degaser, binary pump, autosampler, column oven, and photodiode array detector. An Ascentis® Express F5 column (150 mm × 4.6 mm, 5 µm, Supelco, Sigma Aldrich Chemical Co., St Louis, MO, USA) was used to separate the flavonoids at a temperature of 25 °C. Eluent A was 0.5% acetic acid, and eluent B was 100% acetonitrile. The gradient used for eluent B was 5–12% (0–3 min), 12–25% (3–46 min), 25–90% (46–49.5 min), 90% isocratic (49.5–52 min), 90–5% (52–52.7 min), and 5% isocratic (52.7–59 min). The flow rate was of 0.85 ml min^{-1} and the detection wavelengths were 320 nm, 330 nm, and 370 nm for hydroxycinnamic acid derivatives, acylated flavonol glycosides, and non-acylated flavonol glycosides, respectively. The hydroxycinnamic acid derivatives and glycosides of flavonols were identified as deprotonated molecular ions and characteristic mass fragment ions by HPLC-DAD-ESI-MS^n using an Agilent series 1100 ion trap mass spectrometer in negative ionisation mode.[43] Nitrogen was used as the dry gas (10 L min^{-1}, 325 °C) and the nebulizer gas (40 psi) with a capillary voltage of −3500 V. Helium was used as the collision gas in the ion trap. The mass optimization for the ion optics of the mass spectrometer for quercetin was performed at m/z 301 or arbitrarily at m/z 1000. The MS^n experiments were performed in auto mode up to HPLC-DAD-ESI-MS3 in a scan from m/z 200–2000. Standards (chlorogenic acid, quercertin 3-glucoside, and kaempferol 3-glucoside; Roth, Karlsruhe, Germany) were used for external calibration curves. Results are presented as mg g^{-1} dry matter.

Statistics

For the overview regarding compound groups the data were statistically analysed by a four-factorial ANOVA including the genotype. Fischer's F test was performed to assess the main effect of the factors genotype, day of harvest, PAR intensity and UV radiation as well as their interactions followed by a comparison of the factor levels using Tukey's HSD test. For the specific compounds all data were statistically analysed by a two-factorial ANOVA separately for each genotype (n = 3). Fischer's F test was performed to assess the main effect of the factors PAR intensity and UV radiation and their interactions followed by a comparison of the factor levels using Tukey's HSD test. For non-significant interactions, the means of the levels of the main factors were separated, while for significant interactions, all combinations of the factor levels were compared. Residuals were tested for Gaussian distribution using the Kolmogorov–Smirnov test. All tests were conducted at a significance level of 5%. Calculations were performed using Statistica™ for Windows® (version 13.0, Statsoft Inc., Tulsa, OK, USA).

Results

In the investigated *Arabidopsis thaliana* wild types and UV-signalling mutants fresh matter, dry matter, and leaf area were not affected significantly ($p \leq 0.05$) by the UV condition and UV+PAR intensity (ESI Fig. S1–S3†).

General effects of UV+PAR intensity and UV on flavonoid profiles

The phenolic profiles in the investigated wild types and UV pathway mutants *of Arabidopsis thaliana* are characterized by sinapic acid derivatives with sinapic acid as the main com-

pound as well as non-aclyated quercetin and kaempferol di- and triglycosides containing glucose and rhamnose as glycosylated sugar moieties.

As shown in Table 1, sinapic acid derivatives were affected only by the factor day of harvest while quercetin glycosides were affected by the genotype, PAR intensity and UV condition. Kaempferol glycosides were affected by all 4 factors. There are genotype and day interactions as well as genotype and UV condition interactions for quercetin and kaempferol glycosides. A specific ANOVA reveals that the *hy5-ks50 hyh* double mutant has the lowest concentrations of sinapic acid derivatives, quercetin and kaempferol glycosides, whereas highest concentrations of quercetin and kaempferol glycosides are found in Col-0. Relative to their corresponding wild types, all mutants showed a general tendency to lower levels of quercetin and kaempferol glycosides with significant decrease within the *hy5 ks50 hyh* mutant compared to Ws. On day 3, the concentrations of sinapic acid derivatives and kaempferol glycosides were higher than on day 7. However, higher PAR intensity resulted in higher concentrations of quercetin and kaempferol glycosides. While sinapic acid derivatives were unaffected by the UV conditions for quercetin and kaempferol glycosides, −UV showed lowest concentrations and +UV highest concentrations. Kaempferol glycosides were also increased due to a transfer from a −UV condition to a +UV condition. The transfer of plants from a −UV condition to a +UV condition seems to elicited a fast, initial response that occurs at low PAR intensities in L*er* and Col-0, but this response was delayed in Ler and Ws at high PAR intensities, both of them not significant under the experimental conditions. Exposure to UV radiation, however, had no detectable effect on the flavonoid concentrations in the *uvr8*, *cop1* and *hy5-ks50 hyh* mutants.

Although the highest absolute concentrations of quercetin glycosides were found at +UV conditions in all genotypes regardless of the harvest day and PAR intensity (Fig. 1), a detailed three-way ANOVA for each genotype revealed no significant differences caused by the day of harvest and PAR intensity for any of the genotypes. There are higher concentrations of quercetin glycosides in Ler on day 3, which were grown at higher PAR intensities and +UV conditions, com-

Table 1 Four-factorial ANOVA and Fischer's *F* test was performed to assess the main effect of the factors genotype, day of harvest, PAR intensity and UV condition as well as their interactions followed by a comparison of the factor levels using Tukey's HSD test. ($p \leq 0.05$ ($n = 3$)) for the compound groups sinapic acid derivatives, quercetin glycoside and kaempferol glycosides Lower case letters present significant differences for each factor in sinaoic acid derivatives, quercetin glycosides and kaempferol glycosides

	Sinapic acid derivatives	Quercetin glycosides	Kaempferol glycosides
Genotype	0.060937	0.000000	0.000000
Day	0.024981	0.069713	0.000024
PAR	0.487192	0.000000	0.000000
UV	0.876494	0.000000	0.000000
Genotype × Day	0.552274	0.044656	0.000372
Genotype × PAR	0.526538	0.000000	0.000731
Day × PAR	0.857715	0.406484	0.422900
Genotype × UV	0.692541	0.002676	0.002526
Day × UV	0.505268	0.491601	0.706179
PAR × UV	0.493193	0.161333	0.004423
Genotype × Day × PAR	0.518137	0.433033	0.901807
Genotype × Day × UV	0.800231	0.923412	0.958174
Genotype × PAR × UV	0.660219	0.112113	0.287328
Day × PAR × UV	0.858390	0.843313	0.616821
Genotype × Day × PAR × UV	0.912965	0.997775	0.994295
Genotype			
Ler	a	bc	bc
uvr8	a	ab	b
Col-0	a	d	e
cop1	a	cd	de
Ws	a	bc	cd
hy5-ks50 hyh	a	a	a
Day of harvest			
3	b	a	b
7	a	a	a
PAR intensity			
Low	a	a	a
High	a	b	b
UV condition			
−UV	a	a	a
+UV/−UV	a	a	ab
−UV/+UV	a	a	b
+UV	a	b	b

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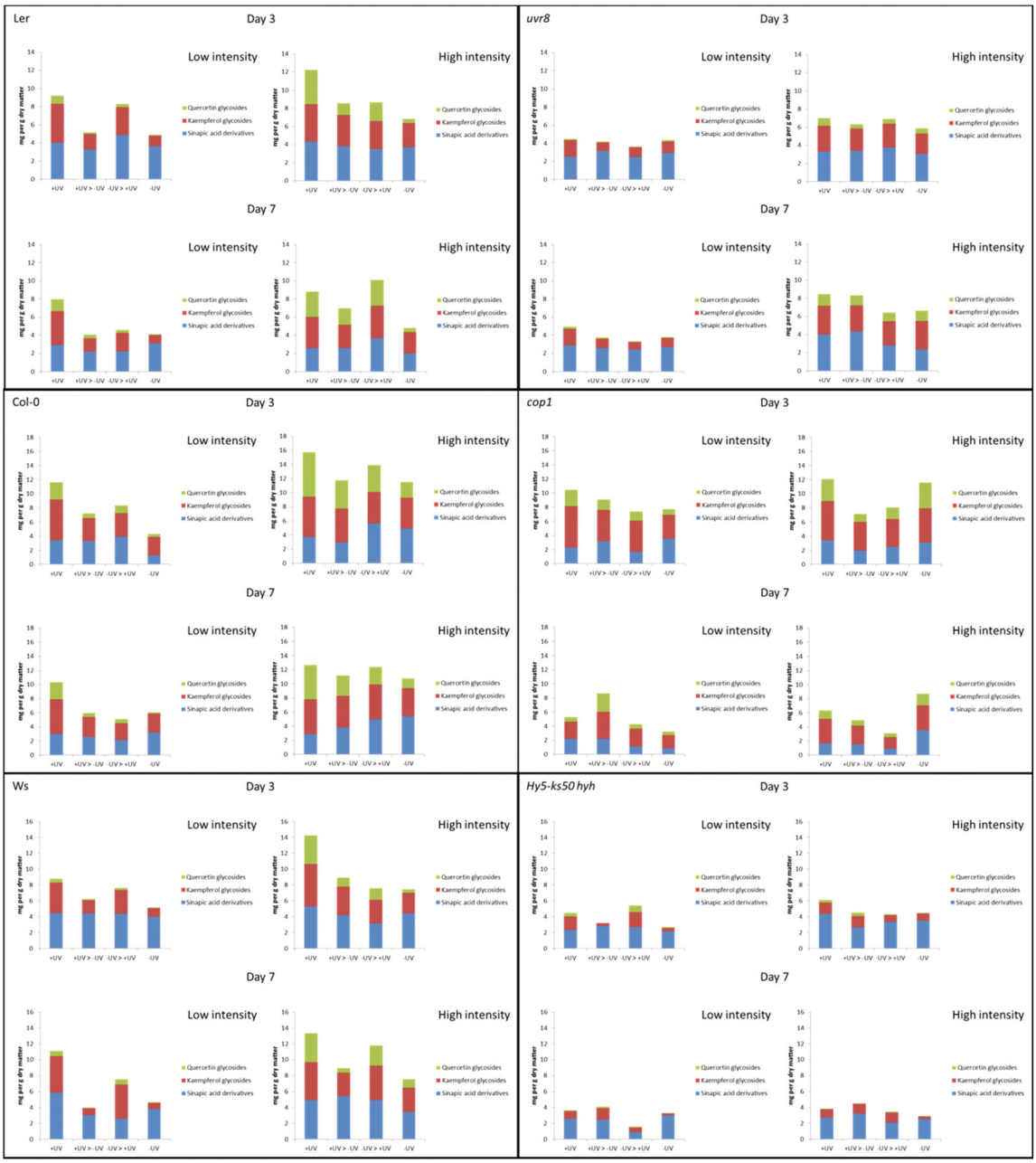

Fig. 1 Phenolic profiles of Landsberg *erecta* (*Ler*) and its *uvr8* mutant (photoreceptor UV Resistance Locus 8), Columbia (Col-0) and its *cop1* mutant (multifunctional E3 ubiquitin ligase Constitutively Photomorphorphogenic 1) and Wassilewskija (Ws) and its *hy5-ks50 hyh* double mutant mutant (bZIP transcription factor Elongated Hypocotyl 5) grown at different UV conditions and intensities at day 3 or day 7 after the transfer of a subset of plants (n = 3).

pared to the −UV conditions. The same was found for kaempferol glycosides, which had higher concentrations only on day 7 in Ws grown at low PAR and +UV conditions and plants transferred from a −UV condition to a +UV condition compared to −UV conditions.

Effects of UV+PAR intensities and UV on quercetin glycosides, kaempferol glycosides and sinapic acid derivatives

On day 3 in the Ler wild type the sinapic acid derivatives were not affected at all, neither by UV+PAR intensities nor by +UV treatment (Table 2). However, of the flavonoid glycosides most compounds responded to high UV+PAR intensities. By comparison, quercetin-3-rutinoside-7-rhamnoside and quercetin-3-rhamnoside-7-rhamnoside and its corresponding kaempferol glycosides, all of which contain two rhamnose moieties in their chemical structure, increased at higher UV+PAR intensities and in the +UV condition. Additionally, all other quercetin glycosides were enhanced by higher UV+PAR intensities but not the +UV treatment. Quecertin-3-diglucoside-7-rhamnoside showed an interaction

Table 2 Influence of UV-B : PAR intensity and UV irradiation on selected hydroxycinnamic acid derivatives and flavonol glycosides (mg g^{-1} dry matter) in *Arabidopsis thaliana* Ler at day 3 and day 7 after a transfer to/from a +UV and −UV condition in low or high UV+PAR intensities. Different letters represent significant differences ($p \leq 0.05$ by Tukey's HSD test ($n = 3$)) for each compound (mean ± standard deviation). SG: sinapoyl-glucoside; SA: sinapic acid; Q: quercetin; K: kaempferol; glc: glucose; rha: rhamnoside; rut: rutinoside (rhamnoglucoside). Different letters show significant differences for the main effects (upper case) and individual effects (lower case). *Significant at $p \leq 0.05$; ** significant at $p \leq 0.01$; *** significant at $p \leq 0.005$; n.s., not significant

Day 3

Intensity	UV	SG	SA	Q-3-rut-7-rha	Q-3-diglc-7-rha	Q-3-rha-7-glc	Q-3-rha-7-rha	K-3-rut-7-rha	K-3-diglc-7-rha	K-3-glc-7-rha	K-3-rha-7-rha	Total flavonoids
Low	+UV	0.71 ± 0.87	3.32 ± 2.25	0.25 ± 0.04	0.23 ± 0.10 a	0.23 ± 0.14	0.21 ± 0.03	1.25 ± 0.03	0.69 ± 0.21	1.03 ± 0.26	1.33 ± 0.15	5.21 ± 0.64
	+UV/−UV	0.27 ± 0.22	3.01 ± 1.90	0.06 ± 0.04	0.06 ± 0.03 a	0.04 ± 0.02	0.04 ± 0.03	1.50 ± 0.20	0.37 ± 0.19	0.27 ± 0.14	0.59 ± 0.18	1.92 ± 0.82
	−UV/+UV	0.31 ± 0.28	4.55 ± 2.82	0.10 ± 0.06	0.08 ± 0.05 a	0.13 ± 0.15	0.06 ± 0.03	0.77 ± 0.35	0.32 ± 0.13	1.09 ± 1.02	0.92 ± 0.32	3.46 ± 2.10
	−UV	0.23 ± 0.11	3.42 ± 2.01	0.04 ± 0.02	0.04 ± 0.02 a	0.03 ± 0.02	0.03 ± 0.03	0.28 ± 0.13	0.19 ± 0.10	0.27 ± 0.21	0.41 ± 0.15	1.29 ± 0.59
High	+UV	0.59 ± 0.16	3.74 ± 2.95	0.91 ± 0.16	0.77 ± 0.21 b	0.98 ± 0.57	1.12 ± 0.19	1.26 ± 0.20	0.52 ± 0.20	0.87 ± 0.39	1.51 ± 0.33	7.93 ± 1.41
	+UV/−UV	0.46 ± 0.27	3.38 ± 1.56	0.37 ± 0.18	0.28 ± 0.07 a	0.29 ± 0.27	0.41 ± 0.26	1.03 ± 0.34	0.50 ± 0.09	0.59 ± 0.28	1.30 ± 0.44	4.77 ± 1.73
	−UV/+UV	0.34 ± 0.19	3.12 ± 2.08	0.52 ± 0.39	0.29 ± 0.19 a	0.84 ± 0.81	0.46 ± 0.64	0.91 ± 0.06	0.40 ± 0.21	0.57 ± 0.23	1.19 ± 0.11	5.18 ± 2.10
	−UV	0.50 ± 0.43	3.21 ± 3.22	0.15 ± 0.10	0.13 ± 0.08 a	0.09 ± 0.05	0.12 ± 0.05	0.70 ± 0.26	0.48 ± 0.11	0.41 ± 0.22	1.08 ± 0.33	3.17 ± 1.04
Main effect												
Intensity	Low	0.38 ± 0.37	3.58 ± 2.24	0.11 ± 0.04 A	0.10 ± 0.05	0.11 ± 0.09 A	0.09 ± 0.03 A	0.70 ± 0.18 A	0.39 ± 0.16	0.66 ± 0.41	0.81 ± 0.20 A	2.97 ± 1.04 A
	High	0.47 ± 0.26	3.38 ± 2.45	0.49 ± 0.21 B	0.37 ± 0.14	0.55 ± 0.43 B	0.53 ± 0.28 B	0.98 ± 0.22 A	0.47 ± 0.15	0.61 ± 0.28	1.27 ± 0.30 B	5.26 ± 1.57 B
UV	+UV	0.65 ± 0.51	3.53 ± 2.60	0.58 ± 0.10 B	0.50 ± 0.16	0.60 ± 0.36	0.66 ± 0.11 B	1.25 ± 0.11 C	0.60 ± 0.20	0.95 ± 0.33	1.42 ± 0.24 B	6.57 ± 1.03 C
	+UV/−UV	0.37 ± 0.25	3.19 ± 1.73	0.21 ± 0.11 AB	0.17 ± 0.05	0.16 ± 0.15	0.23 ± 0.14 AB	0.77 ± 0.27 AB	0.43 ± 0.14	0.43 ± 0.21	0.94 ± 0.31 A	3.34 ± 1.27 AB
	−UV/+UV	0.33 ± 0.24	3.88 ± 2.45	0.31 ± 0.23 AB	0.18 ± 0.12	0.49 ± 0.48	0.26 ± 0.34 AB	0.84 ± 0.21 B	0.36 ± 0.17	0.83 ± 0.62	1.06 ± 0.22 AB	4.32 ± 2.10 BC
	−UV	0.37 ± 0.27	3.31 ± 2.61	0.09 ± 0.06 A	0.08 ± 0.05	0.06 ± 0.04	0.08 ± 0.04 A	0.49 ± 0.19 A	0.34 ± 0.10	0.34 ± 0.21	0.75 ± 0.24 A	2.23 ± 0.81 A
Intensity		n.s.	n.s.	***	***	*	***	*	n.s.	n.s.	***	***
UV		n.s.	n.s.	***	***	n.s.	**	***	n.s.	n.s.	**	***
Intensity × UV		n.s.	n.s.	n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

Day 7

Intensity	UV	SG	SA	Q-3-rut-7-rha	Q-3-diglc-7-rha	Q-3-rha-7-glc	Q-3-rha-7-rha	K-3-rut-7-rha	K-3-diglc-7-rha	K-3-glc-7-rha	K-3-rha-7-rha	Total flavonoids
Low	+UV	0.35 ± 0.28	2.55 ± 1.31	0.29 ± 0.26	0.22 ± 0.10	0.52 ± 0.33	0.32 ± 0.24	1.26 ± 0.35	0.39 ± 0.32	0.78 ± 0.34	1.30 ± 0.48	5.07 ± 1.76
	+UV/−UV	0.42 ± 0.30	1.78 ± 1.32	0.07 ± 0.07	0.09 ± 0.06	0.17 ± 0.16	0.08 ± 0.07	0.45 ± 0.27	0.26 ± 0.28	0.25 ± 0.12	0.50 ± 0.20	1.87 ± 1.06
	−UV/+UV	0.67 ± 0.68	1.53 ± 1.36	0.07 ± 0.07	0.10 ± 0.06	0.08 ± 0.06	0.08 ± 0.06	0.58 ± 0.09	0.45 ± 0.15	0.37 ± 0.16	0.66 ± 0.25	2.39 ± 0.23
	−UV	0.18 ± 0.09	2.92 ± 3.13	0.02 ± 0.01	0.03 ± 0.01	0.02 ± 0.01	0.02 ± 0.01	0.27 ± 0.01	0.19 ± 0.00	0.19 ± 0.08	0.28 ± 0.22	1.02 ± 0.25
High	+UV	0.70 ± 0.63	1.86 ± 0.91	0.61 ± 0.57	0.54 ± 0.18	0.74 ± 0.46	0.94 ± 0.47	1.19 ± 0.29	0.33 ± 0.28	0.64 ± 0.25	1.28 ± 0.29	6.27 ± 2.24
	+UV/−UV	1.13 ± 0.14	1.42 ± 0.13	0.37 ± 0.51	0.33 ± 0.14	0.57 ± 0.66	0.59 ± 0.49	0.77 ± 0.45	0.40 ± 0.09	0.42 ± 0.35	1.00 ± 0.62	4.44 ± 3.29
	−UV/+UV	0.70 ± 0.15	2.97 ± 1.72	0.74 ± 0.60	0.40 ± 0.27	0.97 ± 0.75	0.78 ± 0.56	1.09 ± 0.37	0.42 ± 0.09	0.57 ± 0.27	1.48 ± 0.54	6.46 ± 3.19
	−UV	0.46 ± 0.43	1.53 ± 1.58	0.13 ± 0.19	0.11 ± 0.09	0.08 ± 0.10	0.14 ± 0.16	0.69 ± 0.43	0.41 ± 0.19	0.26 ± 0.23	1.00 ± 0.52	2.82 ± 1.85
Main effect												
Intensity	Low	0.41 ± 0.34	2.20 ± 1.78	0.11 ± 0.10 A	0.11 ± 0.06 A	0.20 ± 0.14 A	0.12 ± 0.09 A	0.64 ± 0.18 A	0.32 ± 0.19	0.40 ± 0.17	0.68 ± 0.29 A	2.58 ± 0.82 A
	High	0.75 ± 0.34	1.94 ± 1.09	0.47 ± 0.47 B	0.34 ± 0.17 B	0.59 ± 0.49 B	0.61 ± 0.42 B	0.93 ± 0.39 B	0.39 ± 0.16	0.47 ± 0.27	1.19 ± 0.49 B	5.00 ± 2.64 B
UV	+UV	0.53 ± 0.45	2.21 ± 1.11	0.45 ± 0.41	0.38 ± 0.14 B	0.63 ± 0.40	0.63 ± 0.36 B	1.22 ± 0.32 C	0.36 ± 0.30	0.71 ± 0.29 B	1.29 ± 0.39 B	5.67 ± 2.00 C
	+UV/−UV	0.78 ± 0.22	1.60 ± 0.73	0.22 ± 0.29	0.21 ± 0.10 A	0.37 ± 0.41	0.33 ± 0.28 AB	0.61 ± 0.36 AB	0.33 ± 0.18	0.34 ± 0.24 A	0.75 ± 0.41 A	3.15 ± 2.18 AB
	−UV/+UV	0.69 ± 0.42	2.25 ± 1.54	0.41 ± 0.33	0.25 ± 0.16 A	0.52 ± 0.41	0.43 ± 0.31 AB	0.83 ± 0.23 B	0.44 ± 0.12	0.47 ± 0.21 AB	1.07 ± 0.39 AB	4.42 ± 1.71 BC
	−UV	0.32 ± 0.26	2.22 ± 2.35	0.08 ± 0.10	0.07 ± 0.05 A	0.05 ± 0.05	0.08 ± 0.08 A	0.48 ± 0.22 A	0.30 ± 0.10	0.22 ± 0.15 A	0.64 ± 0.37 A	1.92 ± 1.05 A
Intensity		n.s.	n.s.	*	***	*	***	*	n.s.	n.s.	**	**
UV		n.s.	n.s.	n.s.	**	n.s.	*	***	n.s.	*	*	*
Intensity × UV		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

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of UV+PAR intensities and +UV condition resulting in its highest concentration at a combination of high UV+PAR intensity and +UV condition. This pattern was, in general, also reflected in the results on day 7. In the *uvr8* mutant of this wild type, there was no effect of the +UV treatment on these quercetin and kaempferol glycosides, but these compounds did increase with higher UV+PAR intensities; the sinapic acid derivatives were not affected by either of these treatments (Table 3).

In the Col-0 wild type, sinapic acid derivatives were not affected by UV+PAR or +UV treatments (Table 4). On day 3, especially the diglycosides quercetin-3-rhamnoside-7-glucoside, quercetin-3-rhamnoside-7-rhamnoside and kaempferol-3-rhamnoside-7-rhamnoside increased in response to higher UV+PAR intensities. At the same time kaempferol-3-rutinoside-7-rhamnoside and kaempferol-3-glucoside-7-rhamnoside, containing only one glucose moiety, were enhanced by the +UV treatment. On day 7, quercetin-3-rutinoside-7-rhamnoside and quercetin-3-rhamnoside-7-rhamnoside and its corresponding kaempferol glycosides, all of which contain two rhamnose moieties in their chemical structure, increased at higher UV+PAR intensities. Three out of four quercetin glycosides were enhanced by higher UV+PAR intensities as well as the +UV treatment. On day 3 in the *cop1* mutant of this wild type, UV+PAR intensity and +UV treatment had no effect on these compounds except for a slight interaction of sinapoyl glucoside leading to high concentrations at low UV+PAR intensities in plants transferred from +UV conditions to −UV conditions (Table 5). However, on day 7 there is an increase of quercetin-3-diglucoside-7-rhamnoside and it corresponding kaempferol glycoside due to low UV+PAR intensities. Sinapic acid was highest at high UV+PAR lacking UV conditions. Furthermore, the diglycosides quercetin-3-rhamnoside-7-glucoside and kaempferol-3-rhamnoside-7-rhamnoside were slightly affected by the UV condition resulting in higher concentrations of the later at high UV+PAR intensities combined with +UV conditions. During emergence prior to the experiment, 75% of the *cop1* mutant plants died and at high UV+PAR intensity we found 8% (1/12) of the plants dead on day 3 and 40% (5/12) of the plants died on day 7.

In Ws wild type, sinapic acid derivatives were not affected by UV+PAR intensities and +UV treatment (Table 6). All quercetin glycosides and kaempferol-3-rutinoside-7-rhamnoside and kaempferol-3-rhamnoside-7-rhamnoside, both of which contain two rhamnose moieties in their chemical structure, increased at higher UV+PAR intensities on day 3. Additionally, two quercetin glycosides and three out of four kaempferol glycosides were enhanced by the +UV treatment at this time. Interestingly, on day 7 quercetin glycosides were mainly affected by higher UV+PAR intensity whereas the presence of UV was a main driver of increases in keampferol glycosides. In the *hy5-ks50 hyh* double mutant of this wild type, there was no effect of the higher UV+PAR intensities or the +UV treatment in any of the phenolic compounds investigated (Table 7).

Discussion

Phenolic compounds, including hydroxycinnamic acid derivatives and flavonoids, are one of the major compound groups involved in plant protection against high UV and PAR exposure.[20] In this study we found that wild types of *Arabidopsis thaliana*; Ler, Col-0 and Ws had comparable concentrations of total phenolic compounds. There was a higher absolute concentrations of quercetin and kaempferol glycosides in the high UV+PAR intensity plants, including UV-A and UV-B, and, consequently, lower induction of phenolic compounds when plants adapted to a higher PAR were transferred to a +UV condition (−UV > +UV). This is in line with findings in tobacco that highlight the priming effect of high PAR.[44] Nevertheless, in all wild types, the plants grown under constant +UV conditions had higher phenolic compound concentrations, while the plants grown under constant −UV conditions had lower phenolic concentrations and the plants that were transferred from one UV condition to the other showed intermediate concentrations. This reflects the fundamental understanding of the role played by phenolic compounds as shielding components and antioxidants.[21,45] Quercetin glycosides increased most in the +UV-treated *Arabidopsis thaliana* wild types. These compounds may serve an important role as antioxidants due to the catechol structure in the B-ring compared to kaempferol, which lacks this chemical trait. In general, quercetin glycosides appear to be a much more UV-specific and responsive pool of compounds than other phenolics. These findings are consistent with a previous study reported rapid, diurnal changes in quercetin glycosides in field-grown okra (*Abelmoschus esculentus*).[46]

Our results confirm that the UVR8 photoreceptor plays a key role in mediating flavonoid responses to UV radiation. In our study, the concentration of phenolic compounds between the wild type L*er* and the *uvr8* mutant was comparable in the absence of UV radiation. However, when these plants were exposed to UV radiation, phenolic concentrations in the *uvr8* mutant were approximately half that of the Ler wild type. As other studies in controlled environments have shown, the perception of UV by the UVR8 photoreceptor therefore is critical for the induction of flavonoid biosynthesis.[12,15,47] In an outdoor study, UVR8 is required for the plant's response to UV including higher expression of genes linked to flavonoid synthesis (*e.g.* CHS, TT7 (F3′H), and DFR) and consequently the adaptation to +UV conditions.[13]

Results of our study, which found that elevated concentrations of phenolic compounds were observed in treatment with higher UV+PAR intensity, also indicate a priming effect of PAR on these compounds. These results are consistent with previous field studies on *Vicia faba* and *Populus tremuloides* that full induction of UV-absorbing compounds requires UV-B, UV-A and PAR.[48] These findings also confirm that not only the ratio of UV to PAR, but also the absolute intensities are the triggers for the accumulation of phenolic compound.[38] The increased concentrations of phenolic compounds resulting from higher UV+PAR intensities may be a consequence of (1)

Table 3 Influence of UV-B : PAR intensity and UV on selected hydroxycinnamic acid derivatives and flavonol glycosides (mg g^{-1} dry matter) in *Arabidopsis thaliana uvr8* (mutant of Ler) at day 3 and day 7 after a transfer to/from a +UV and −UV condition in low or high UV+PAR intensities. Different letters represent significant differences ($p \leq 0.05$ by Tukey's HSD test ($n = 3$)) for each compound (mean ± standard deviation). SG: sinapoyl glucoside; SA: sinapic acid; Q: quercetin; K: kaempferol; glc: glucose; rha: rhamnoside; rut: rutinoside (rhamnoglucoside). Different letters show significant differences for the main effects (upper case) and individual effects (lower case). *Significant at $p \leq 0.05$; ** significant at $p \leq 0.01$; ***significant at $p \leq 0.005$; n.s., not significant

Day 3

Intensity	UV	SG	SA	Q-3-rut-7-rha	Q-3-diglc-7-rha	Q-3-rha-7-glc	Q-3-rha-7-rha	K-3-rut-7-rha	K-3-diglc-7-rha	K-3-glc-7-rha	K-3-rha-7-rha	Total flavonoids
Low	+UV	0.23 ± 0.22	2.30 ± 2.24	0.05 ± 0.02	0.04 ± 0.02	0.04 ± 0.03	0.03 ± 0.02	0.48 ± 0.09	0.30 ± 0.08	0.38 ± 0.30	0.69 ± 0.07	2.54 ± 0.53
	+UV/−UV	0.25 ± 0.33	2.91 ± 1.53	0.03 ± 0.02	0.03 ± 0.02	0.02 ± 0.02	0.02 ± 0.01	0.24 ± 0.13	0.17 ± 0.06	0.18 ± 0.17	0.36 ± 0.13	1.19 ± 0.54
	−UV/+UV	0.19 ± 0.12	2.31 ± 1.95	0.03 ± 0.03	0.03 ± 0.02	0.02 ± 0.02	0.02 ± 0.01	0.28 ± 0.13	0.18 ± 0.09	0.21 ± 0.18	0.41 ± 0.13	1.45 ± 0.53
	−UV	0.25 ± 0.31	2.71 ± 1.95	0.06 ± 0.08	0.05 ± 0.07	0.05 ± 0.08	0.05 ± 0.08	0.31 ± 0.27	0.24 ± 0.22	0.25 ± 0.31	0.45 ± 0.23	1.87 ± 1.33
High	+UV	0.42 ± 0.17	2.91 ± 2.62	0.23 ± 0.16	0.17 ± 0.09	0.22 ± 0.28	0.23 ± 0.22	0.77 ± 0.39	0.43 ± 0.11	0.46 ± 0.40	1.17 ± 0.65	4.19 ± 2.25
	+UV/−UV	0.23 ± 0.17	3.17 ± 2.54	0.14 ± 0.10	0.11 ± 0.08	0.10 ± 0.07	0.12 ± 0.08	0.66 ± 0.18	0.43 ± 0.08	0.37 ± 0.16	1.01 ± 0.25	3.33 ± 0.81
	−UV/+UV	0.44 ± 0.22	3.33 ± 2.68	0.18 ± 0.12	0.13 ± 0.08	0.11 ± 0.07	0.13 ± 0.10	0.75 ± 0.26	0.47 ± 0.07	0.40 ± 0.14	1.01 ± 0.34	2.89 ± 1.19
	−UV	0.41 ± 0.38	2.66 ± 2.12	0.15 ± 0.13	0.12 ± 0.08	0.13 ± 0.14	0.16 ± 0.16	0.60 ± 0.30	0.36 ± 0.08	0.35 ± 0.18	0.93 ± 0.38	3.53 ± 1.36
Main effect												
Intensity	Low	0.23 ± 0.24	2.56 ± 1.92	0.04 ± 0.04 A	0.04 ± 0.03 A	0.03 ± 0.04 A	0.03 ± 0.03 A	0.33 ± 0.15 A	0.22 ± 0.11 A	0.25 ± 0.24	0.48 ± 0.14 A	1.76 ± 0.73 A
	High	0.38 ± 0.23	3.02 ± 2.49	0.18 ± 0.13 B	0.13 ± 0.08 B	0.14 ± 0.14 B	0.16 ± 0.14 B	0.69 ± 0.28 B	0.42 ± 0.09 B	0.39 ± 0.22	1.03 ± 0.41 B	3.49 ± 1.40 B
UV	+UV	0.32 ± 0.20	2.61 ± 2.43	0.14 ± 0.09	0.10 ± 0.06	0.13 ± 0.16	0.13 ± 0.12	0.62 ± 0.24	0.37 ± 0.09	0.42 ± 0.35	0.93 ± 0.36	3.37 ± 1.39
	+UV/−UV	0.25 ± 0.25	3.04 ± 2.03	0.08 ± 0.06	0.07 ± 0.05	0.06 ± 0.05	0.07 ± 0.04	0.45 ± 0.15	0.30 ± 0.07	0.27 ± 0.16	0.69 ± 0.19	2.26 ± 0.68
	−UV/+UV	0.32 ± 0.17	2.82 ± 2.32	0.11 ± 0.08	0.08 ± 0.05	0.07 ± 0.04	0.07 ± 0.06	0.51 ± 0.20	0.32 ± 0.08	0.30 ± 0.16	0.71 ± 0.24	2.17 ± 0.86
	−UV	0.33 ± 0.34	2.69 ± 2.03	0.11 ± 0.11	0.09 ± 0.08	0.09 ± 0.11	0.10 ± 0.12	0.46 ± 0.29	0.30 ± 0.15	0.30 ± 0.25	0.69 ± 0.30	2.70 ± 1.35
Intensity		n.s.	n.s.	***	***	*	***	***	***	n.s.	***	***
UV		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Intensity × UV		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

Day 7

Intensity	UV	SG	SA	Q-3-rut-7-rha	Q-3-diglc-7-rha	Q-3-rha-7-glc	Q-3-rha-7-rha	K-3-rut-7-rha	K-3-diglc-7-rha	K-3-glc-7-rha	K-3-rha-7-rha	Total flavonoids
Low	+UV	0.20 ± 0.12	2.67 ± 1.09	0.05 ± 0.04	0.04 ± 0.02	0.04 ± 0.03	0.12 ± 0.18	0.49 ± 0.33	0.32 ± 0.14	0.28 ± 0.19	0.75 ± 0.51	2.31 ± 1.14
	+UV/−UV	0.26 ± 0.20	2.33 ± 1.06	0.04 ± 0.05	0.05 ± 0.03	0.03 ± 0.03	0.03 ± 0.04	0.28 ± 0.20	0.21 ± 0.13	0.15 ± 0.10	0.41 ± 0.25	1.32 ± 0.82
	−UV/+UV	0.29 ± 0.42	2.14 ± 0.70	0.02 ± 0.00	0.03 ± 0.02	0.02 ± 0.02	0.02 ± 0.01	0.25 ± 0.08	0.18 ± 0.05	0.12 ± 0.04	0.25 ± 0.17	0.86 ± 0.02
	−UV	0.34 ± 0.49	2.36 ± 0.86	0.03 ± 0.00	0.03 ± 0.01	0.02 ± 0.01	0.02 ± 0.01	0.26 ± 0.04	0.21 ± 0.08	0.14 ± 0.01	0.40 ± 0.01	1.09 ± 0.17
High	+UV	0.69 ± 0.49	3.31 ± 1.83	0.34 ± 0.31	0.22 ± 0.15	0.37 ± 0.39	0.40 ± 0.35	0.85 ± 0.33	0.44 ± 0.11	0.50 ± 0.13	1.37 ± 0.49	4.70 ± 2.14
	+UV/−UV	0.49 ± 0.47	3.83 ± 1.98	0.27 ± 0.28	0.19 ± 0.12	0.33 ± 0.48	0.34 ± 0.34	0.78 ± 0.26	0.41 ± 0.08	0.48 ± 0.14	1.22 ± 0.35	4.48 ± 1.99
	−UV/+UV	0.37 ± 0.12	2.43 ± 2.30	0.16 ± 0.16	0.15 ± 0.03	0.31 ± 0.21	0.33 ± 0.17	0.78 ± 0.61	0.44 ± 0.40	0.39 ± 0.36	1.05 ± 0.89	3.62 ± 2.22
	−UV	0.52 ± 0.48	1.82 ± 1.70	0.26 ± 0.29	0.20 ± 0.13	0.33 ± 0.51	0.34 ± 0.38	0.86 ± 0.25	0.47 ± 0.09	0.51 ± 0.21	1.32 ± 0.33	4.53 ± 2.11
Main effect												
Intensity	Low	0.27 ± 0.31	2.37 ± 0.93	0.04 ± 0.02 A	0.04 ± 0.02 A	0.03 ± 0.02 A	0.05 ± 0.06 A	0.32 ± 0.16 A	0.23 ± 0.10 A	0.17 ± 0.09 A	0.45 ± 0.24 A	1.40 ± 0.54 A
	High	0.52 ± 0.39	2.85 ± 1.95	0.26 ± 0.26 B	0.19 ± 0.11 B	0.34 ± 0.40 B	0.35 ± 0.31 B	0.81 ± 0.36 B	0.44 ± 0.17 B	0.47 ± 0.21 B	1.24 ± 0.51 B	4.33 ± 2.11 B
UV	+UV	0.44 ± 0.30	2.99 ± 1.46	0.20 ± 0.18	0.13 ± 0.08	0.20 ± 0.21	0.26 ± 0.26	0.67 ± 0.33	0.38 ± 0.12	0.39 ± 0.16	1.06 ± 0.50	3.51 ± 1.64
	+UV/−UV	0.38 ± 0.34	3.08 ± 1.52	0.16 ± 0.17	0.12 ± 0.07	0.18 ± 0.26	0.18 ± 0.19	0.53 ± 0.23	0.31 ± 0.10	0.32 ± 0.12	0.81 ± 0.30	2.90 ± 1.40
	−UV/+UV	0.33 ± 0.27	2.28 ± 1.50	0.09 ± 0.08	0.09 ± 0.02	0.16 ± 0.12	0.18 ± 0.09	0.51 ± 0.37	0.31 ± 0.23	0.26 ± 0.20	0.65 ± 0.53	2.24 ± 1.12
	−UV	0.43 ± 0.49	2.09 ± 1.28	0.15 ± 0.15	0.11 ± 0.07	0.18 ± 0.26	0.18 ± 0.20	0.56 ± 0.15	0.34 ± 0.08	0.32 ± 0.11	0.86 ± 0.17	2.81 ± 1.14
Intensity		n.s.	n.s.	**	***	**	***	***	**	***	***	***
UV		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Intensity × UV		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

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Table 4 Influence of UV-B : PAR intensity and UV on selected hydroxycinnamic acid derivatives and flavonol glycosides (mg g^{-1} dry matter) in *Arabidopsis thaliana* Col-0 at day 3 and day 7 after a transfer to/from a +UV and −UV condition in low or high UV+PAR intensities. Different letters represent significant differences ($p \leq 0.05$ by Tukey's HSD test ($n = 3$)) for each compound (mean ± standard deviation). SG: sinapoyl-glucoside; SA: sinapic acid; Q: quercetin; K: kaempferol; glc: glucose; rha: rhamnoside; rut: rutinoside (rhamnoglucoside). Different letters show significant differences for the main effects (upper case) and individual effects (lower case). *Significant at $p \leq 0.05$; **significant at $p \leq 0.01$; ***significant at $p \leq 0.005$; n.s., not significant

Day 3

Intensity	UV	SG	SA	Q-3-rut-7-rha	Q-3-diglc-7-rha	Q-3-rha-7-glc	Q-3-rha-7-rha	K-3-rut-7-rha	K-3-diglc-7-rha	K-3-glc-7-rha	K-3-rha-7-rha	Total flavonoids
Low	+UV	1.47 ± 1.24	1.95 ± 0.90	0.67 ± 0.50	0.02 ± 0.01	1.21 ± 0.88	0.55 ± 0.39	1.80 ± 0.32	0.03 ± 0.02	1.92 ± 0.30	1.98 ± 0.37	8.19 ± 2.58
	+UV/−UV	0.50 ± 0.40	2.82 ± 2.66	0.21 ± 0.26	0.04 ± 0.02	0.28 ± 0.36	0.15 ± 0.18	1.05 ± 0.67	0.04 ± 0.03	0.97 ± 0.66	1.20 ± 0.72	3.95 ± 2.81
	−UV/+UV	0.82 ± 0.89	3.23 ± 3.26	0.28 ± 0.21	0.03 ± 0.01	0.54 ± 0.48	0.27 ± 0.22	0.97 ± 0.31	0.03 ± 0.02	1.12 ± 0.42	1.17 ± 0.31	4.41 ± 1.94
	−UV	0.71 ± 0.48	0.61 ± 0.61	0.13 ± 0.15	0.05 ± 0.04	0.17 ± 0.19	0.08 ± 0.08	0.77 ± 0.61	0.06 ± 0.06	0.81 ± 0.61	1.02 ± 0.75	3.09 ± 2.47
High	+UV	0.99 ± 0.44	2.74 ± 0.97	1.70 ± 1.04	0.03 ± 0.02	3.06 ± 1.78	1.56 ± 0.74	1.81 ± 0.22	0.04 ± 0.05	1.75 ± 0.59	2.06 ± 0.49	12.02 ± 3.78
	+UV/−UV	0.84 ± 0.65	2.15 ± 1.21	1.18 ± 1.38	0.03 ± 0.03	1.81 ± 1.99	1.02 ± 1.07	1.49 ± 0.35	0.05 ± 0.05	1.41 ± 0.39	1.78 ± 0.34	8.77 ± 4.98
	−UV/+UV	0.82 ± 0.71	4.85 ± 4.28	0.99 ± 0.33	0.03 ± 0.02	1.81 ± 0.86	1.02 ± 0.26	1.40 ± 0.18	0.03 ± 0.03	1.27 ± 0.33	1.73 ± 0.31	8.27 ± 1.92
	−UV	0.71 ± 0.59	4.25 ± 1.29	0.66 ± 0.62	0.04 ± 0.04	1.04 ± 0.94	0.52 ± 0.43	1.29 ± 0.21	0.06 ± 0.07	1.21 ± 0.12	1.75 ± 0.11	6.58 ± 2.45
Main effect												
Intensity	Low	0.82 ± 0.75	2.15 ± 1.85	0.32 ± 0.28	0.04 ± 0.02	0.55 ± 0.48 A	0.26 ± 0.22 A	1.15 ± 0.448	0.04 ± 0.03	1.21 ± 0.50	1.35 ± 0.53 A	4.91 ± 2.45 A
	High	0.84 ± 0.60	3.50 ± 1.94	1.13 ± 0.84	0.03 ± 0.03	1.93 ± 1.39 B	1.03 ± 0.63 B	1.50 ± 0.24	0.05 ± 0.05	1.41 ± 0.36	1.83 ± 0.31 B	8.91 ± 3.29 B
UV	+UV	1.23 ± 0.84	2.35 ± 0.94	1.18 ± 0.77	0.03 ± 0.02	2.14 ± 1.33	1.06 ± 0.57	1.81 ± 0.27 B	0.04 ± 0.03	1.83 ± 0.45 B	2.02 ± 0.43	10.10 ± 3.18
	+UV/−UV	0.67 ± 0.53	2.48 ± 1.93	0.70 ± 0.82	0.04 ± 0.02	1.04 ± 1.17	0.58 ± 0.62	1.27 ± 0.51 AB	0.04 ± 0.04	1.19 ± 0.52 AB	1.49 ± 0.52	6.36 ± 3.90
	−UV/+UV	0.77 ± 0.80	4.04 ± 3.77	0.63 ± 0.27	0.03 ± 0.02	1.17 ± 0.66	0.64 ± 0.24	1.19 ± 0.25 A	0.03 ± 0.02	1.20 ± 0.38 AB	1.45 ± 0.31	6.34 ± 1.93
	−UV	0.66 ± 0.53	2.43 ± 0.95	0.40 ± 0.39	0.05 ± 0.04	0.60 ± 0.57	0.30 ± 0.25	1.03 ± 0.41 A	0.06 ± 0.07	1.01 ± 0.37 A	1.39 ± 0.43	4.83 ± 2.46
Intensity		n.s.	n.s.	n.s.	n.s.	**	***	n.s.	n.s.	n.s.	*	**
UV		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.	*	n.s.	n.s.
Intensity × UV		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

Day 7

Intensity	UV	SG	SA	Q-3-rut-7-rha	Q-3-diglc-7-rha	Q-3-rha-7-glc	Q-3-rha-7-rha	K-3-rut-7-rha	K-3-diglc-7-rha	K-3-glc-7-rha	K-3-rha-7-rha	Total flavonoids
Low	+UV	1.10 ± 1.45	1.90 ± 1.13	0.68 ± 0.47	0.02 ± 0.01	1.16 ± 0.72	0.58 ± 0.33	1.58 ± 0.59	0.03 ± 0.01	1.57 ± 0.55	1.73 ± 0.65	7.34 ± 3.33
	+UV/−UV	0.40 ± 0.34	2.19 ± 1.50	0.20 ± 0.25	0.04 ± 0.04	0.24 ± 0.30	0.12 ± 0.15	0.88 ± 0.70	0.04 ± 0.04	0.86 ± 0.63	1.02 ± 0.70	3.40 ± 2.77
	−UV/+UV	0.69 ± 0.81	1.47 ± 1.02	0.33 ± 0.39	0.05 ± 0.10	0.14 ± 0.12	0.09 ± 0.04	0.64 ± 0.47	0.08 ± 0.10	0.61 ± 0.48	1.04 ± 0.20	2.97 ± 1.01
	−UV	0.42 ± 0.49	2.80 ± 2.24	0.06 ± 0.02	0.03 ± 0.02	0.08 ± 0.04	0.04 ± 0.01	0.77 ± 0.29	0.03 ± 0.02	0.77 ± 0.24	1.10 ± 0.38	2.88 ± 0.93
High	+UV	0.86 ± 0.82	2.04 ± 1.73	1.44 ± 0.48	0.02 ± 0.03	2.09 ± 0.93	1.32 ± 0.25	1.74 ± 0.36	0.04 ± 0.03	1.30 ± 0.30	1.86 ± 0.29	9.81 ± 2.51
	+UV/−UV	0.68 ± 0.28	3.16 ± 2.48	0.82 ± 0.65	0.03 ± 0.01	1.39 ± 1.10	0.72 ± 0.55	1.37 ± 0.22	0.03 ± 0.01	1.29 ± 0.31	1.75 ± 0.17	7.40 ± 2.85
	−UV/+UV	0.36 ± 0.16	4.62 ± 3.02	0.68 ± 0.42	0.05 ± 0.04	1.13 ± 0.78	0.65 ± 0.39	1.54 ± 0.49	0.04 ± 0.04	1.46 ± 0.57	1.91 ± 0.58	7.48 ± 3.25
	−UV	0.71 ± 0.17	4.72 ± 2.65	0.42 ± 0.28	0.04 ± 0.00	0.63 ± 0.39	0.32 ± 0.17	1.21 ± 0.32	0.02 ± 0.00	1.09 ± 0.14	1.65 ± 0.24	5.37 ± 1.52
Main effect												
Intensity	Low	0.65 ± 0.77	2.09 ± 1.47	0.32 ± 0.28 A	0.04 ± 0.02	0.41 ± 0.30 A	0.21 ± 0.13 A	0.97 ± 0.51 A	0.04 ± 0.04	0.95 ± 0.48	1.22 ± 0.48 A	4.15 ± 2.01 A
	High	0.65 ± 0.36	3.64 ± 2.47	0.84 ± 0.46 B	0.03 ± 0.02	1.31 ± 0.80 B	0.75 ± 0.34 B	1.47 ± 0.35 B	0.03 ± 0.02	1.29 ± 0.33	1.79 ± 0.32 B	7.51 ± 2.53 B
UV	+UV	0.98 ± 1.13	1.97 ± 1.43	1.04 ± 0.48 B	0.02 ± 0.01	1.43 ± 0.83 B	0.95 ± 0.29 B	1.66 ± 0.47	0.03 ± 0.02	1.43 ± 0.43	1.79 ± 0.47	8.58 ± 2.92 A
	+UV/−UV	0.54 ± 0.31	2.68 ± 1.99	0.51 ± 0.45 AB	0.03 ± 0.02	1.08 ± 0.70 AB	0.42 ± 0.35 AB	1.13 ± 0.46	0.03 ± 0.03	1.08 ± 0.47	1.39 ± 0.43	5.40 ± 2.81 A
	−UV/+UV	0.53 ± 0.49	3.05 ± 2.02	0.51 ± 0.40 AB	0.05 ± 0.04	1.03 ± 0.45 AB	0.37 ± 0.22 AB	1.09 ± 0.48	0.06 ± 0.07	1.03 ± 0.53	1.48 ± 0.39	5.22 ± 2.13 A
	−UV	0.56 ± 0.33	3.76 ± 2.44	0.24 ± 0.15 A	0.04 ± 0.02	0.93 ± 0.22 A	0.18 ± 0.09 A	0.99 ± 0.31	0.02 ± 0.01	0.93 ± 0.19	1.38 ± 0.31	4.13 ± 1.22 A
Intensity		n.s.	n.s.	**	n.s.	***	***	*	n.s.	n.s.	**	***
UV		n.s.	n.s.	*	n.s.	*	***	n.s.	n.s.	n.s.	n.s.	*
Intensity × UV		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

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Table 5 Influence of UV-B : PAR intensity and UV on selected hydroxycinnamic acid derivatives and flavonol glycosides (mg g^{-1} dry matter) in *Arabidopsis thaliana cop1* (mutant of Col-0) at day 3 and day 7 after a transfer to/from a +UV and −UV condition in low or high UV+PAR intensities. Different letters represent significant differences ($p \leq 0.05$ by Tukey's HSD test ($n = 3$)) for each compound (mean ± standard deviation). SG: sinapoyl-glucoside; SA: sinapic acid; Q: quercetin; K: kaempferol; glc: glucose; rha: rhamnoside; rut: rutinoside (rhamnoglucoside). Different letters show significant differences for the main effects (upper case) and individual effects (lower case). *Significant at $p \leq 0.05$; **significant at $p \leq 0.01$; ***significant at $p \leq 0.005$; n.s., not significant

Day 3

Intensity	UV	SG	SA	Q-3-rut-7-rha	Q-3-diglc-7-rha	Q-3-rha-7-glc	Q-3-rha-7-rha	K-3-rut-7-rha	K-3-diglc-7-rha	K-3-glc-7-rha	K-3-rha-7-rha	Total flavonoids
Low	+UV	1.31 ± 0.07 ab	1.01 ± 0.33	0.63 ± 0.00	0.29 ± 0.40	0.93 ± 0.96	0.52 ± 0.09	1.70 ± 0.35	0.51 ± 0.72	1.99 ± 0.92	1.80 ± 0.33	9.72 ± 1.53
	+UV/−UV	1.84 ± 0.49 b	1.87 ± 0.67	0.41 ± 0.58	0.21 ± 0.40	0.48 ± 0.57	0.37 ± 0.54	1.36 ± 0.85	0.37 ± 0.71	1.25 ± 0.62	1.43 ± 0.68	7.69 ± 4.95
	−UV/+UV	0.81 ± 0.92 ab	0.86 ± 1.13	0.35 ± 0.36	0.20 ± 0.20	0.43 ± 0.47	0.32 ± 0.30	1.29 ± 1.64	0.36 ± 0.36	1.49 ± 1.91	1.27 ± 1.58	5.72 ± 6.83
	−UV	0.34 ± 0.45 ab	3.21 ± 4.03	0.23 ± 0.36	0.10 ± 0.13	0.30 ± 0.44	0.21 ± 0.32	0.97 ± 0.73	0.16 ± 0.26	1.04 ± 0.84	1.18 ± 0.73	4.80 ± 3.62
High	+UV	0.72 ± 0.71 ab	2.68 ± 1.77	0.88 ± 0.47	0.22 ± 0.18	1.26 ± 0.84	0.83 ± 0.37	1.67 ± 0.14	0.36 ± 0.30	1.60 ± 0.34	1.87 ± 0.35	8.70 ± 1.96
	+UV/−UV	0.24 ± 0.25 a	1.72 ± 1.08	0.33 ± 0.01	0.03 ± 0.00	0.39 ± 0.09	0.40 ± 0.14	1.27 ± 0.21	0.04 ± 0.03	0.97 ± 0.44	1.77 ± 0.01	5.20 ± 0.66
	−UV/+UV	0.45 ± 0.54 ab	2.01 ± 1.30	0.46 ± 0.30	0.10 ± 0.19	0.57 ± 0.40	0.50 ± 0.28	1.21 ± 0.44	0.16 ± 0.34	1.05 ± 0.55	1.54 ± 0.43	6.07 ± 2.61
	−UV	0.66 ± 0.75 ab	2.43 ± 2.31	1.03 ± 1.03	0.18 ± 0.24	1.39 ± 1.21	1.05 ± 0.90	1.46 ± 0.56	0.28 ± 0.45	1.22 ± 0.50	1.87 ± 0.39	8.48 ± 5.25
Main effect												
Intensity	Low	0.94 ± 0.48	1.74 ± 1.54	0.41 ± 0.33	0.20 ± 0.28	0.54 ± 0.61	0.36 ± 0.31	1.33 ± 0.89	0.35 ± 0.51	1.39 ± 1.07	1.42 ± 0.83	6.98 ± 4.23
	High	0.52 ± 0.5+	2.21 ± 1.61	0.67 ± 0.45	0.13 ± 0.15	0.90 ± 0.64	0.70 ± 0.42	1.41 ± 0.34	0.21 ± 0.28	1.21 ± 0.46	1.76 ± 0.30	7.11 ± 2.62
UV	+UV	1.02 ± 0.39	1.85 ± 1.05	0.76 ± 0.24	0.26 ± 0.29	1.09 ± 0.90	0.68 ± 0.23	1.68 ± 0.25	0.43 ± 0.51	1.68 ± 0.63	1.83 ± 0.34	9.21 ± 1.75
	+UV/−UV	0.76 ± 0.37	1.80 ± 0.87	0.37 ± 0.30	0.12 ± 0.20	0.43 ± 0.33	0.39 ± 0.34	1.32 ± 0.53	0.21 ± 0.37	1.11 ± 0.53	1.60 ± 0.34	6.44 ± 2.81
	−UV/+UV	0.63 ± 0.73	1.44 ± 1.22	0.40 ± 0.33	0.15 ± 0.20	0.50 ± 0.44	0.41 ± 0.29	1.25 ± 1.04	0.26 ± 0.35	1.27 ± 1.23	1.41 ± 1.01	5.89 ± 4.72
	−UV	0.50 ± 0.60	2.82 ± 3.17	0.63 ± 0.70	0.14 ± 0.19	0.84 ± 0.82	0.63 ± 0.61	1.22 ± 0.65	0.22 ± 0.36	1.13 ± 0.67	1.53 ± 0.56	6.64 ± 4.43
Intensity		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
UV		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Intensity × UV		*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

Day 7

Intensity	UV	SG	SA	Q-3-rut-7-rha	Q-3-diglc-7-rha	Q-3-rha-7-glc	Q-3-rha-7-rha	K-3-rut-7-rha	K-3-diglc-7-rha	K-3-glc-7-rha	K-3-rha-7-rha	Total flavonoids
Low	+UV	0.36 ± 0.52	1.86 ± 0.81 bcd	0.21 ± 0.24 ab	0.11 ± 0.15	0.20 ± 0.21	0.17 ± 0.15 ab	0.72 ± 0.62	0.19 ± 0.27	0.63 ± 0.63	0.89 ± 0.76 ab	3.17 ± 2.97
	+UV/−UV	0.68 ± 0.27	0.36 ± 0.24 a	0.79 ± 1.02 b	0.24 ± 0.09	0.82 ± 1.26	0.81 ± 1.21 b	1.16 ± 0.81	0.42 ± 0.16	0.98 ± 0.665	1.27 ± 0.89 ab	7.46 ± 6.09
	−UV/+UV	0.39 ± 0.48	0.76 ± 0.70 abc	0.21 ± 0.20 ab	0.14 ± 0.17	0.18 ± 0.14	0.16 ± 0.15 a	0.78 ± 0.21	0.24 ± 0.30	0.62 ± 0.22	0.87 ± 0.19 ab	3.18 ± 1.55
	−UV	0.32 ± 0.18	0.55 ± 0.40 ab	0.14 ± 0.16 a	0.10 ± 0.10	0.16 ± 0.15	0.14 ± 0.15 a	0.55 ± 0.48	0.17 ± 0.18	0.47 ± 0.47	0.67 ± 0.55 ab	2.39 ± 2.22
High	+UV	0.08 ± 0.00	1.57 ± 0.00 cd	0.35 ± 0.00 ab	0.02 ± 0.00	0.36 ± 0.00	0.51 ± 0.00 ab	1.08 ± 0.00	0.03 ± 0.00	0.73 ± 0.00	1.62 ± 0.00 b	4.70 ± 0.00
	+UV/−UV	0.06 ± 0.00	1.48 ± 0.00 cd	0.23 ± 0.00 ab	0.01 ± 0.00	0.24 ± 0.00	0.34 ± 0.00 ab	0.80 ± 0.00	0.02 ± 0.00	0.56 ± 0.00	1.25 ± 0.00 ab	3.44 ± 0.00
	−UV/+UV	0.27 ± 0.23	0.61 ± 0.33 ab	0.16 ± 0.01 ab	0.09 ± 0.09	0.15 ± 0.00	0.18 ± 0.04 a	0.49 ± 0.31	0.16 ± 0.15	0.35 ± 0.11	0.63 ± 0.52 a	2.22 ± 0.75
	−UV	0.19 ± 0.00	3.37 ± 0.00 d	0.53 ± 0.00 ab	0.02 ± 0.00	0.50 ± 0.00	0.65 ± 0.00 ab	1.12 ± 0.00	0.02 ± 0.00	0.82 ± 0.00	1.53 ± 0.00 ab	4.13 ± 0.00
Main effect												
Intensity	Low	0.44 ± 0.36	1.17 ± 0.54	0.34 ± 0.41	0.14 ± 0.13 B	0.34 ± 0.44	0.32 ± 0.42	0.80 ± 0.53	0.26 ± 0.23 B	0.67 ± 0.49	0.92 ± 0.60	4.05 ± 3.20
	High	0.15 ± 0.06	1.76 ± 0.08	0.32 ± 0.00	0.04 ± 0.02 A	0.31 ± 0.00	0.42 ± 0.01	0.87 ± 0.08	0.06 ± 0.04 A	0.61 ± 0.03	1.26 ± 0.13	3.67 ± 0.19
UV	+UV	0.22 ± 0.26	1.72 ± 0.41	0.28 ± 0.12	0.06 ± 0.08	0.28 ± 1.11 A	0.34 ± 0.08	0.90 ± 0.31	0.11 ± 0.13	0.68 ± 0.31 A	1.26 ± 0.38	3.94 ± 1.49
	+UV/−UV	0.37 ± 0.13	1.50 ± 0.12	0.51 ± 0.51	0.13 ± 0.05	0.53 ± 0.63 A	0.57 ± 0.60	0.98 ± 0.40	0.22 ± 0.08	0.77 ± 0.40 A	1.26 ± 0.44	5.45 ± 3.04
	−UV/+UV	0.33 ± 0.36	0.68 ± 0.52	0.18 ± 0.11	0.11 ± 0.13	0.17 ± 0.07 A	0.17 ± 0.10	0.63 ± 0.26	0.20 ± 0.26	0.48 ± 0.26 A	0.75 ± 0.35	2.70 ± 1.15
	−UV	0.25 ± 0.09	1.96 ± 0.20	0.34 ± 0.08	0.06 ± 0.05	0.33 ± 0.08 A	0.40 ± 0.07	0.84 ± 0.24	0.09 ± 0.09	0.64 ± 0.24 A	1.10 ± 0.28	3.35 ± 1.11
Intensity		***	***	n.s.	***	n.s.	n.s.	n.s.	***	n.s.	n.s.	n.s.
UV		n.s.	***	n.s.	n.s.	*	n.s.	n.s.	n.s.	n.s.	*	n.s.
Intensity × UV		n.s.	***	*	n.s.	n.s.	*	n.s.	n.s.	n.s.	*	n.s.

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Table 6 Influence of UV-B : PAR intensity and UV on selected hydroxycinnamic acid derivatives and flavonol glycosides (mg g^{-1} dry matter) in *Arabidopsis thalaiana* Ws at day 3 and day 7 after a transfer to/from a +UV and −UV condition in low or high UV+PAR intensities. Different letters represent significant differences ($p \leq 0.05$ by Tukey's HSD test ($n = 3$)) for each compound (mean ± standard deviation). SG: sinapoyl-glucoside; SA: sinapic acid; Q: quercetin; K: kaempferol; glc: glucose; rha: rhamnoside; rut: rutinoside (rhamnoglucoside). Different letters show significant differences for the main effects (upper case) and individual effects (lower case). *Significant at $p \leq 0.05$; ** significant at $p \leq 0.01$; *** significant at $p \leq 0.005$; n.s., not significant

Day 3

Intensity	UV	SG	SA	Q-3-rut-7-rha	Q-3-diglc-7-rha	Q-3-rha-7-glc	Q-3-rha-7-rha	K-3-rut-7-rha	K-3-diglc-7-rha	K-3-glc-7-rha	K-3-rha-7-rha	Total flavonoids
Low	+UV	0.58 ± 1.08	3.85 ± 3.64	0.11 ± 0.10	0.16 ± 0.12	0.15 ± 0.10	0.11 ± 0.04	1.16 ± 0.16	0.63 ± 0.26	0.95 ± 0.41	1.09 ± 0.21	5.54 ± 0.41
	+UV/−UV	0.29 ± 0.31	4.10 ± 4.24	0.04 ± 0.02	0.07 ± 0.05	0.03 ± 0.02	0.03 ± 0.02	0.53 ± 0.19	0.40 ± 0.20	0.19 ± 0.05	0.54 ± 0.20	1.83 ± 0.74
	−UV/+UV	0.35 ± 0.55	3.99 ± 4.30	0.10 ± 0.14	0.09 ± 0.13	0.08 ± 0.10	0.07 ± 0.09	0.85 ± 0.52	0.55 ± 0.46	0.74 ± 0.42	0.84 ± 0.42	4.23 ± 2.25
	−UV	0.12 ± 0.07	3.83 ± 3.05	0.02 ± 0.01	0.02 ± 0.01	0.02 ± 0.01	0.01 ± 0.00	0.30 ± 0.12	0.23 ± 0.09	0.15 ± 0.13	0.44 ± 0.15	1.30 ± 0.49
High	+UV	0.50 ± 0.03	4.80 ± 2.03	0.97 ± 0.58	0.68 ± 0.33	1.16 ± 0.83	0.82 ± 0.40	1.71 ± 0.30	0.65 ± 0.27	1.28 ± 0.47	1.70 ± 0.20	8.97 ± 2.58
	+UV/−UV	0.29 ± 0.26	3.89 ± 2.89	0.34 ± 0.21	0.29 ± 0.16	0.27 ± 0.11	0.26 ± 0.12	1.11 ± 0.36	0.58 ± 0.31	0.71 ± 0.29	1.17 ± 0.26	5.63 ± 1.30
	−UV/+UV	0.34 ± 0.51	2.82 ± 2.81	0.39 ± 0.65	0.26 ± 0.33	0.56 ± 1.13	0.30 ± 0.47	0.90 ± 0.63	0.39 ± 0.33	0.60 ± 0.43	1.03 ± 0.65	5.73 ± 4.09
	−UV	0.23 ± 0.26	4.16 ± 3.23	0.16 ± 0.20	0.13 ± 0.13	0.10 ± 0.10	0.08 ± 0.10	0.82 ± 0.46	0.28 ± 0.27	0.46 ± 0.26	1.04 ± 0.43	3.67 ± 1.38
Main effect												
Intensity	Low	0.33 ± 0.50	3.94 ± 3.81	0.07 ± 0.07 A	0.09 ± 0.08 A	0.07 ± 0.06 A	0.06 ± 0.04 A	0.71 ± 0.25 A	0.45 ± 0.25	0.51 ± 0.25	0.73 ± 0.25 A	3.23 ± 0.97 A
	High	0.34 ± 0.26	3.92 ± 2.74	0.46 ± 0.41 B	0.34 ± 0.24 B	0.52 ± 0.54 B	0.36 ± 0.27 B	1.14 ± 0.44 B	0.48 ± 0.29	0.76 ± 0.36	1.24 ± 0.38 B	6.00 ± 2.34 B
UV	+UV	0.54 ± 0.56	4.32 ± 2.83	0.54 ± 0.34	0.42 ± 0.22 A	0.06 ± 0.47	0.47 ± 0.22 A	1.44 ± 0.23 B	0.64 ± 0.26	1.11 ± 0.44 B	1.40 ± 0.20 A	7.26 ± 1.49 B
	+UV/−UV	0.29 ± 0.28	4.00 ± 3.57	0.19 ± 0.12	0.18 ± 0.11 A	0.15 ± 0.07	0.15 ± 0.07 A	0.82 ± 0.28 AB	0.49 ± 0.26	0.45 ± 0.17 A	0.86 ± 0.23 A	3.73 ± 1.02 AB
	−UV/+UV	0.35 ± 0.53	3.40 ± 3.55	0.24 ± 0.39	0.17 ± 0.23 A	0.32 ± 0.61	0.18 ± 0.28 A	0.88 ± 0.58 AB	0.47 ± 0.39	0.67 ± 0.43 AB	0.93 ± 0.53 A	4.98 ± 3.17 AB
	−UV	0.17 ± 0.17	3.99 ± 3.14	0.09 ± 0.10	0.07 ± 0.07 A	0.06 ± 0.05	0.04 ± 0.05 A	0.56 ± 0.29 A	0.26 ± 0.18	0.30 ± 0.19 A	0.74 ± 0.29 A	2.49 ± 0.94 A
Intensity		n.s.	n.s.	**	***	*	***	*	n.s.	n.s.	***	***
UV		n.s.	n.s.	n.s.	*	n.s.	*	**	n.s.	***	*	**
Intensity × UV		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

Day 7

Intensity	UV	SG	SA	Q-3-rut-7-rha	Q-3-diglc-7-rha	Q-3-rha-7-glc	Q-3-rha-7-rha	K-3-rut-7-rha	K-3-diglc-7-rha	K-3-glc-7-rha	K-3-rha-7-rha	Total flavonoids
Low	+UV	0.25 ± 0.18	5.61 ± 3.36	0.19 ± 0.19	0.18 ± 0.05	0.18 ± 0.19	0.15 ± 0.09	1.45 ± 0.54	0.71 ± 0.12 d	1.09 ± 0.74	1.32 ± 0.54	5.94 ± 2.38
	+UV/−UV	0.25 ± 0.39	2.81 ± 1.25	0.02 ± 0.01	0.03 ± 0.02	0.02 ± 0.01	0.02 ± 0.01	0.27 ± 0.09	0.19 ± 0.09 ab	0.10 ± 0.06	0.28 ± 0.08	1.08 ± 0.29
	−UV/+UV	0.50 ± 0.56	2.08 ± 0.28	0.19 ± 0.01	0.16 ± 0.05	0.17 ± 0.05	0.17 ± 0.05	1.27 ± 0.75	0.75 ± 0.03 cd	1.05 ± 0.81	1.20 ± 0.69	4.95 ± 2.06
	−UV	0.34 ± 0.33	3.49 ± 1.97	0.04 ± 0.05	0.02 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	0.22 ± 0.08	0.18 ± 0.10 a	0.07 ± 0.02	0.29 ± 0.34	0.92 ± 0.58
High	+UV	1.01 ± 0.43	3.94 ± 1.07	0.90 ± 0.76	0.70 ± 0.34	1.26 ± 0.94	0.82 ± 0.52	1.49 ± 0.34	0.67 ± 0.24 bcd	1.05 ± 0.59	1.50 ± 0.41	7.73 ± 3.47
	+UV/−UV	0.28 ± 0.03	5.17 ± 3.22	0.18 ± 0.17	0.14 ± 0.06	0.17 ± 0.14	0.11 ± 0.08	0.87 ± 0.18	0.44 ± 0.08 abcd	0.55 ± 0.17	1.04 ± 0.19	3.73 ± 0.85
	−UV/+UV	0.24 ± 0.23	4.70 ± 3.28	0.66 ± 0.22	0.44 ± 0.21	0.87 ± 0.49	0.57 ± 0.24	1.34 ± 0.06	0.52 ± 0.08 abcd	1.03 ± 0.13	1.44 ± 0.04	6.87 ± 1.11
	−UV	0.45 ± 0.38	2.98 ± 0.71	0.32 ± 0.33	0.23 ± 0.29	0.33 ± 0.30	0.19 ± 0.25	0.89 ± 0.57	0.44 ± 0.18 abc	0.61 ± 0.40	1.09 ± 0.44	4.06 ± 2.66
Main effect												
Intensity	Low	0.34 ± 0.36	3.50 ± 1.72	0.11 ± 0.06 A	0.10 ± 0.03 A	0.10 ± 0.06 A	0.09 ± 0.04 A	0.80 ± 0.37	0.46 ± 0.09	0.58 ± 0.41	0.77 ± 0.41 A	3.23 ± 1.33 A
	High	0.50 ± 0.27	4.20 ± 2.07	0.51 ± 0.37 B	0.38 ± 0.22 B	0.66 ± 0.47 B	0.42 ± 0.27 B	1.15 ± 0.29	0.52 ± 0.15	0.81 ± 0.32	1.27 ± 0.27 B	5.60 ± 2.02 B
UV	+UV	0.63 ± 0.30	4.78 ± 2.22	0.54 ± 0.47	0.44 ± 0.20 A	0.72 ± 0.57	0.48 ± 0.30 B	1.47 ± 0.44 B	0.69 ± 0.18	1.07 ± 0.67 C	1.41 ± 0.47 B	6.84 ± 2.93 C
	+UV/−UV	0.27 ± 0.21	3.99 ± 2.23	0.10 ± 0.09	0.09 ± 0.04 A	0.10 ± 0.07	0.07 ± 0.04 A	0.57 ± 0.13 A	0.32 ± 0.09	0.32 ± 0.12 AB	0.66 ± 0.13 A	2.41 ± 0.57 A
	−UV/+UV	0.37 ± 0.39	3.39 ± 1.78	0.43 ± 0.11	0.30 ± 0.13 A	0.52 ± 0.27	0.37 ± 0.14 B	1.31 ± 0.40 B	0.63 ± 0.06	1.04 ± 0.47 BC	1.32 ± 0.37 AB	5.91 ± 1.58 BC
	−UV	0.40 ± 0.36	3.24 ± 1.34	0.18 ± 0.19	0.13 ± 0.15 A	0.17 ± 0.16	0.10 ± 0.13 A	0.55 ± 0.32 A	0.31 ± 0.14	0.34 ± 0.21 A	0.69 ± 0.39 A	2.49 ± 1.62 AB
Intensity		n.s.	n.s.	**	***	***	***	n.s.	n.s.	n.s.	**	**
UV		n.s.	n.s.	n.s.	**	n.s.	**	***	***	***	***	***
Intensity × UV		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**	n.s.	n.s.	n.s.

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Table 7 Influence of UV-B : PAR intensity and UV on selected hydroxycinnamic acid derivatives and flavonol glycosides (mg g^{-1} dry matter) in *Arabidopsis thaliana hy5-ks50 hyh* (double mutant of Ws) at day 3 and day 7 after a transfer to/from a +UV and −UV condition in low or high UV+PAR intensities. Different letters represent significant differences ($p \leq 0.05$ by Tukey's HSD test ($n = 3$)) for each compound (mean ± standard deviation). SG: sinapoyl-glucoside; SA: sinapic acid; Q: quercetin; K: kaempferol; glc: glucose; rha: rhamnoside; rut: rutinoside (rhamnoglucoside). Different letters show significant differences for the main effects (upper case) and individual effects (lower case). *Significant at $p \leq 0.05$; ** significant at $p \leq 0.01$; *** significant at $p \leq 0.005$; n.s., not significant

Day 3

Intensity	UV	SG	SA	Q-3-rut-7-rha	Q-3-diglc-7-rha	Q-3-rha-7-glc	Q-3-rha-7-rha	K-3-rut-7-rha	K-3-diglc-7-rha	K-3-glc-7-rha	K-3-rha-7-rha	Total flavonoids
Low	+UV	0.35 ± 0.38	1.94 ± 0.85	0.13 ± 0.16	0.13 ± 0.16	0.13 ± 0.16	0.12 ± 0.16	0.43 ± 0.16	0.32 ± 0.21	0.30 ± 0.18	0.65 ± 0.15	2.79 ± 1.15
	+UV/−UV	0.07 ± 0.04	2.75 ± 2.58	0.01 ± 0.01	0.02 ± 0.02	0.01 ± 0.01	0.01 ± 0.01	0.08 ± 0.04	0.06 ± 0.03	0.05 ± 0.01	0.14 ± 0.06	0.45 ± 0.16
	−UV/+UV	0.54 ± 0.46	2.12 ± 1.91	0.16 ± 0.16	0.19 ± 0.16	0.27 ± 0.16	0.19 ± 0.16	0.52 ± 0.42	0.42 ± 0.33	0.37 ± 0.31	0.60 ± 0.46	2.76 ± 2.15
	−UV	0.10 ± 0.06	2.02 ± 2.51	0.03 ± 0.02	0.03 ± 0.02	0.03 ± 0.03	0.06 ± 0.09	0.13 ± 0.09	0.09 ± 0.07	0.07 ± 0.02	0.14 ± 0.06	0.68 ± 0.31
High	+UV	0.28 ± 0.31	4.06 ± 5.00	0.06 ± 0.11	0.06 ± 0.11	0.09 ± 0.11	0.09 ± 0.11	0.35 ± 0.29	0.28 ± 0.27	0.21 ± 0.17	0.59 ± 0.40	1.78 ± 1.55
	+UV/−UV	0.35 ± 0.35	2.28 ± 2.35	0.12 ± 0.15	0.11 ± 0.15	0.11 ± 0.16	0.11 ± 0.16	0.35 ± 0.20	0.30 ± 0.26	0.24 ± 0.24	0.54 ± 0.15	1.89 ± 1.41
	−UV/+UV	0.18 ± 0.26	3.12 ± 3.12	0.04 ± 0.05	0.03 ± 0.03	0.02 ± 0.02	0.03 ± 0.03	0.23 ± 0.28	0.11 ± 0.10	0.10 ± 0.11	0.43 ± 0.45	1.28 ± 1.07
	−UV	0.13 ± 0.15	3.36 ± 3.37	0.03 ± 0.04	0.03 ± 0.03	0.03 ± 0.04	0.03 ± 0.03	0.21 ± 0.12	0.14 ± 0.10	0.11 ± 0.04	0.41 ± 0.12	1.26 ± 0.53
Main effect												
Intensity	Low	0.27 ± 0.24	2.21 ± 1.96	0.09 ± 0.09	0.09 ± 0.09	0.11 ± 0.09	0.10 ± 0.11	0.29 ± 0.18	0.22 ± 0.16	0.20 ± 0.13	0.38 ± 0.18	1.67 ± 0.94
	High	0.24 ± 0.27	3.21 ± 3.46	0.07 ± 0.09	0.07 ± 0.08	0.06 ± 0.08	0.06 ± 0.08	0.29 ± 0.22	0.21 ± 0.18	0.16 ± 0.14	0.50 ± 0.28	1.55 ± 1.14
UV	+UV	0.31 ± 0.35	3.00 ± 2.92	0.11 ± 0.13	0.11 ± 0.13	0.11 ± 01.13	0.11 ± 0.14	0.39 ± 0.22	0.30 ± 0.24	0.25 ± 0.17	0.70 ± 0.27 A	2.28 ± 1.35
	+UV/−UV	0.21 ± 0.20	2.51 ± 2.47	0.06 ± 0.08	0.07 ± 0.09	0.06 ± 0.08	0.06 ± 0.08	0.21 ± 0.12	0.18 ± 0.14	0.14 ± 0.12	0.36 ± 0.11 A	1.17 ± 0.78
	−UV/+UV	0.36 ± 0.36	2.62 ± 2.52	0.12 ± 0.11	0.11 ± 0.09	0.15 ± 0.09	0.11 ± 0.10	0.37 ± 0.35	0.26 ± 0.22	0.24 ± 0.21	0.59 ± 0.45 A	2.02 ± 1.61
	−UV	0.12 ± 0.10	2.69 ± 2.94	0.03 ± 0.03	0.03 ± 0.03	0.03 ± 0.04	0.04 ± 0.06	0.17 ± 0.11	0.11 ± 0.08	0.09 ± 0.03	0.33 ± 0.09 A	0.97 ± 0.42
Intensity		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
UV		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.
Intensity × UV		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

Day 7

Intensity	UV	SG	SA	Q-3-rut-7-rha	Q-3-diglc-7-rha	Q-3-rha-7-glc	Q-3-rha-7-rha	K-3-rut-7-rha	K-3-diglc-7-rha	K-3-glc-7-rha	K-3-rha-7-rha	Total flavonoids
Low	+UV	0.50 ± 0.98	2.09 ± 1.47	0.02 ± 0.00	0.03 ± 0.02	0.02 ± 0.01	0.02 ± 0.01	0.27 ± 0.17	0.17 ± 0.12	0.11 ± 0.05	0.43 ± 0.17	1.27 ± 0.52
	+UV/−UV	0.32 ± 0.61	2.15 ± 1.87	0.05 ± 0.09	0.08 ± 0.17	0.05 ± 0.09	0.05 ± 0.09	0.35 ± 0.61	0.27 ± 0.52	0.20 ± 0.34	0.64 ± 1.13	2.17 ± 3.04
	−UV/+UV	0.09 ± 0.08	0.78 ± 0.31	0.03 ± 0.03	0.03 ± 00.04	0.03 ± 0.04	0.03 ± 0.04	0.16 ± 0.07	0.10 ± 0.06	0.09 ± 0.03	0.27 ± 0.15	0.89 ± 0.31
	−UV	0.08 ± 0.05	2.94 ± 2.54	0.01 ± 0.00	0.02 ± 0.01	0.01 ± 0.00	0.01 ± 0.00	0.06 ± 0.00	0.04 ± 0.01	0.04 ± 0.00	0.11 ± 0.00	0.26 ± 0.03
High	+UV	0.12 ± 0.01	2.63 ± 0.13	0.02 ± 0.01	0.02 ± 0.01	0.02 ± 0.00	0.02 ± 0.01	0.27 ± 0.03	0.16 ± 0.05	0.11 ± 0.03	0.50 ± 0.12	1.51 ± 0.20
	+UV/−UV	0.16 ± 0.10	3.08 ± 1.47	0.03 ± 0.02	0.03 ± 0.02	0.02 ± 0.01	0.02 ± 0.02	0.30 ± 0.19	0.18 ± 0.13	0.14 ± 0.08	0.59 ± 0.35	1.34 ± 0.76
	−UV/+UV	0.10 ± 0.05	2.03 ± 0.03	0.05 ± 0.03	0.03 ± 0.02	0.03 ± 0.01	0.03 ± 0.02	0.32 ± 0.10	0.18 ± 0.07	0.12 ± 0.02	0.62 ± 0.22	1.17 ± 0.48
	−UV	0.09 ± 0.05	2.45 ± 1.39	0.01 ± 0.01	0.01 ± 0.00	0.01 ± 0.00	0.01 ± 0.00	0.09 ± 0.01	0.05 ± 0.01	0.04 ± 0.01	0.19 ± 0.03	0.41 ± 0.06
Main effect												
Intensity	Low	0.25 ± 0.43	1.99 ± 1.55	0.02 ± 0.03	0.04 ± 0.06	0.03 ± 0.03	0.03 ± 0.03	0.21 ± 0.21	0.15 ± 0.18	0.11 ± 0.11	0.36 ± 0.36	1.15 ± 0.98
	High	0.12 ± 0.05	2.55 ± 0.76	0.03 ± 0.02	0.02 ± 0.01	0.02 ± 0.01	0.02 ± 0.01	0.25 ± 0.08	0.15 ± 0.07	0.10 ± 0.03	0.48 ± 0.18	1.11 ± 0.38
UV	+UV	0.31 ± 0.49	2.36 ± 0.80	0.02 ± 0.01	0.02 ± 0.01	0.02 ± 0.01	0.02 ± 0.01	0.27 ± 0.10	0.17 ± 0.09	0.11 ± 0.04	0.47 ± 0.15	1.39 ± 0.36
	+UV/−UV	0.24 ± 0.36	2.62 ± 1.67	0.04 ± 0.05	0.06 ± 0.10	0.03 ± 0.05	0.03 ± 0.05	0.33 ± 0.40	0.23 ± 0.32	0.17 ± 0.21	0.62 ± 0.74	1.75 ± 1.90
	−UV/+UV	0.10 ± 0.06	1.41 ± 0.17	0.04 ± 0.3	0.03 ± 0.03	0.03 ± 0.03	0.03 ± 0.03	0.24 ± 0.08	0.14 ± 0.06	0.10 ± 0.02	0.44 ± 0.18	1.03 ± 0.40
	−UV	0.09 ± 0.05	2.69 ± 1.96	0.01 ± 0.00	0.01 ± 0.01	0.01 ± 0.00	0.01 ± 0.00	0.08 ± 0.00	0.05 ± 0.01	0.04 ± 0.01	0.15 ± 0.02	0.33 ± 0.04
Intensity		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
UV		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Intensity × UV		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

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higher ROS in the plant tissues, generally due to strong exposure to light, resulting in an increased demand for the biosynthesis of phenolics as antioxidants,[31] and/or (2) the downstream COP1 required for the nuclear accumulation of UVR8[49] constitutively interacts with cryptochromes that are activated due to the higher PAR levels [6]. Consequently, the loss of COP1, which plays a key role in many light-signalling pathways, has a huge impact on the acclimation to higher UV and PAR intensities. *Cop1* mutants had high mortality in high UV+PAR intensities on day 7 to plants in low UV+PAR intensities. It has been demonstrated that COP1 is required for photomorphogenesis and stress acclimation in *Arabidopsis thaliana.*[16,50] In the present study, *cop1* mutants had comparable phenolic concentrations at both high and low UV+PAR intensities and were not affected by UV irradiation. It is possible that high ROS levels lead to these high phenolic concentrations and only plants with already high phenolic concentrations were able to survive high UV+PAR intensities. Compared with the wild type Col-0, which showed the typical pattern towards light treatment, the *cop1* mutant was comparable to a slightly lower concentration of phenolic compounds, which also underlines the hypothesis above. COP1 is described as stabilizing the transcription factors HY5 and HYH,[15,51] both of which are responsible for the UVR8-mediated UV response in plants.[52] HY5, together with MYB12, regulates the expression of genes involved in flavonoid biosynthesis (*e.g.* CHS, F3′H and DFR)[51,53] and consequently lead to the increase of specific metabolites such as quercetin glycosides, which are shown in the present study for the wild type Ws, whereas a knock-out of HY5 resulted in the loss of the ability to respond to higher UV+PAR intensities, as well as UV, and consequently to very low concentrations of phenolic compounds in the *hy5-ks50 hyh* double mutant.

The introduction of UV at low UV+PAR intensities generally led to the tendency increase of quercetin and kaemferol glycosides on day 3, whereas at high UV+PAR intensities increases occurred only on day 7. These findings indirectly support (1) the suggestion that these compounds serve an important role as antioxidants[11] and (2) the influence that priming with high PAR may have.[44] However, it is possible that elevated levels of ROS are present at higher UV+PAR intensities and the oxidation of flavonoids masks their biosynthesis in the first days. The analysis of gene expression from 1 to 7 days would provide insights into this hypothesis. In Ler, the more complex triglycosides of quercetin and kaemferol, such as quercetin-3-rutinoside-7-rhamnoside, responded to the introduction of UV at low UV+PAR intensities on day 3, while for the delayed response at high UV+PAR intensities it was mainly kaempferol-3-rutinoside-7-rhamnoside. In contrast, in Col-0 the response of kaempferol glycosides was low at low UV+PAR intensities but mainly quercetin-3-rhamnoside-7-rhamnoside contributed to a delayed response at high UV+PAR intensities. A similar pattern can be found for Ws, where mainly kaempferol-3-glucoside-7-rhamnoside was increased at low UV+PAR intensities after the introduction of UV on day 3 whereas all kaempferol glycosides and quercetin-3-rhamnoside-7-rhamnoside as well as quercetin-3-diglucoside-7-rhamnoside were increased in a delayed response at high UV+PAR intensities. This leads to the conclusion that both quercetin and kaempferol glycosides fulfill essential roles in the acclimation to UV irradiation[11,25] and the synthesis does not only depend on the chemical structure (*e.g.* catechol structure) but also on the species and thus the interaction with other metabolites and morphological traits. Further studies are needed to evaluate the functional significance of these relatively rapid *vs.* slow responses in flavonoid compounds. However, our results are consistent with a number of field and laboratory observations that point to a UV acclimation response in plants that is temporally dynamic over timescales ranging from hours to days.[37]

Conclusion

Our results indicate that UVR8, COP1 and HY5 all play an important role in the accumulation of flavonoids as a response to UV irradiation. The absence of any one of these UV-signalling components results in the plant being unable to enrich flavonoids in response to UV irradiation; very low flavonoid concentrations were observed in the *hy5-ks50 hyh* double mutants. The present study further reveals that flavonoid accumulation in *Arabidopsis thaliana* is triggered by UV and higher UV+PAR intensity at comparable UV : PAR ratios. *Arabidopsis thaliana* wild types show a well-known pattern of light response by increasing their flavonoids due to higher UV+PAR intensity and +UV conditions. However, the catechol structure in quercetin appears to be less important than the glycosylation pattern, *e.g.* having 2 rhamnose moieties. At low UV+PAR intensities the introduction of UV leads to an initial tendency increase of flavonoids in the wild types after 3 days, while at high UV+PAR intensities this response was delayed to day 7. Both quercetin and kaempferol glycosides contributed to the adaptation to UV, but these compounds appear to differ in the time course of their production and accumulation.

Conflicts of interest

There is no conflict of interest.

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