UV-B responses in the spotlight: Dynamic photoreceptorinterplay and cell-type specificity

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Abstract

Plants are constantly exposed to a multitude of external signals, including light. The information contained within the full spectrum of light is perceived by a battery of photoreceptors, each with specific and shared signalling outputs. Recently, it has become clear that UV-B radiation is a vital component of the electromagnetic spectrum, guiding growth and being crucial for plant fitness. However, given the large overlap between UV-B specific signalling pathways and other photoreceptors, understanding how plants can distinguish UV-B specific signals from other light components deserves more scrutiny. With recent evidence, we propose that UV-B signalling and other light signalling pathways occur within distinct tissues and cell-types and that the contribution of each pathway depends on the type of response and the developmental stage of the plant. Elucidating the precise site(s) of action of each molecular player within these signalling pathways is key to fully understand how plants are able to orchestrate coordinated responses to light within the whole plant body. Focusing our efforts on the molecular study of light signal interactions to understand plant growth in natural environments in a cell-type specific manner will be a next step in the field of photobiology.

KEYWORDS
auxin, etiolation, growth, photobiology, phototropism, UV Radiation

1 | UV-B SIGNALLING IS AN IMPORTANT INDUCER OF PHOTOMORPHOGENIC GROWTH

Light is a vital part of plant life, providing the energy contained within photons to synthesise chemical energy to drive metabolic and developmental processes. Plants evolved to derive information from light intensity and quality (i.e., the spectral distribution of light), to optimise their development by fine-tuning growth and metabolism, or by deploying survival strategies (de Wit et al., 2016). Through specific photoreceptor signalling pathways, higher plants can perceive and integrate information from visible light (400–750 nm), but also from the ultraviolet (UV) part of the spectrum (280—400 nm; Galvão & Fankhauser, 2015). Though UV light constitutes only a fraction of the solar spectrum reaching

the earth's surface, these wavelengths, especially UV-B, can have deleterious effects on plant life due to their high-energetic character. The biological effects of UV-B are often dose- dependent (Mintoff et al., 2014). At high doses UV-B becomes harmful, leading to DNA and protein damage (Britt, 1995), the disruption of the photosynthetic machinery (Sztatelman et al., 2015), and the accumulation of reactive oxygen species (Frohnmeyer & Staiger, 2003). At moderate doses, however, plants can activate a series of regulatory mechanisms as part of the photomorphogenic programme to mitigate UV-damage (Frohnmeyer & Staiger, 2003; Vanhaelewyn et al., 2016a; Vanhaelewyn et al., 2020). As much as

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photosynthetically active radiation alters plant development, UV-B also brings about a series of morphological and developmental changes, such as the inhibition of growth, increased root/shoot ratio, and phototropic bending (Jenkins, 2017). Unlike UV-B, UV-A irradiation is generally not damaging for plants, but photo- morphogenic responses have been observed. These include altera- tions in stem and petiole elongation, as well induction of flavonoids(Qian et al., 2021; Vanhaelewyn et al., 2020). Nevertheless, with the exception of a few recent studies (Brelsford et al., 2019; Raiet al., 2020), the molecular basis for UV-A responses is relatively unchartered territory.

To date, one UV-B specific photoreceptor has been identified: the β-propeller protein UV RESISTANCE LOCUS 8 (UVR8; Kliebenstein et al., 2002; Rizzini et al., 2011). In the absence of UV-B light, UVR8 photoreceptors occur as homodimers within the cytosol (or nucleus). In the nucleus, on the other hand, the E3 ligase CONSTITUTIVE PHOTOMORPHOGENIC (COP1) forms a complex with SUPPRESSOR OF PHYA-105 1 (SPA1), SPA2, SPA3 and SPA4

proteins and targets photomorphogenesis-related transcription factors such as ELONGATED HYPOCOTYL 5 (HY5) for proteasomal degradation (Figure 1; Heijde & Binkert, Yin, et al., 2013; Huanget al., 2013; Rizzini et al., 2011; Yin et al., 2015). UV-B light excitestryptophan residues within the predominantly cytoplasmic UVR8, leading to its monomerization and facilitating its subsequent nuclear translocation (Christie et al., 2012; Fang et al., 2022; Kaiserli & Jenkins, 2007). In the nucleus, two distinct domains of the UVR8 protein directly interact with COP1, namely the β-propeller and C27 domains (Favory et al., 2009; Wang et al., 2022; Yin et al., 2015). This interaction effectively inactivates the COP1-SPA complex (Favory et al., 2009; Oravecz et al., 2006). UVR8 directly competeswith COP1 substrates and abolishes its E3 ligase function (Huanget al., 2013; Lau et al., 2019). In addition, UVR8-COP1 binding is required for UVR8 nuclear accumulation and retention (Fang et al., 2022; Yin et al., 2016). As a result, in the absence of active COP1, the central basic leucine zipper transcription factors HY5 and HY5 HOMOLOG (HYH)—which are essential for light signalling

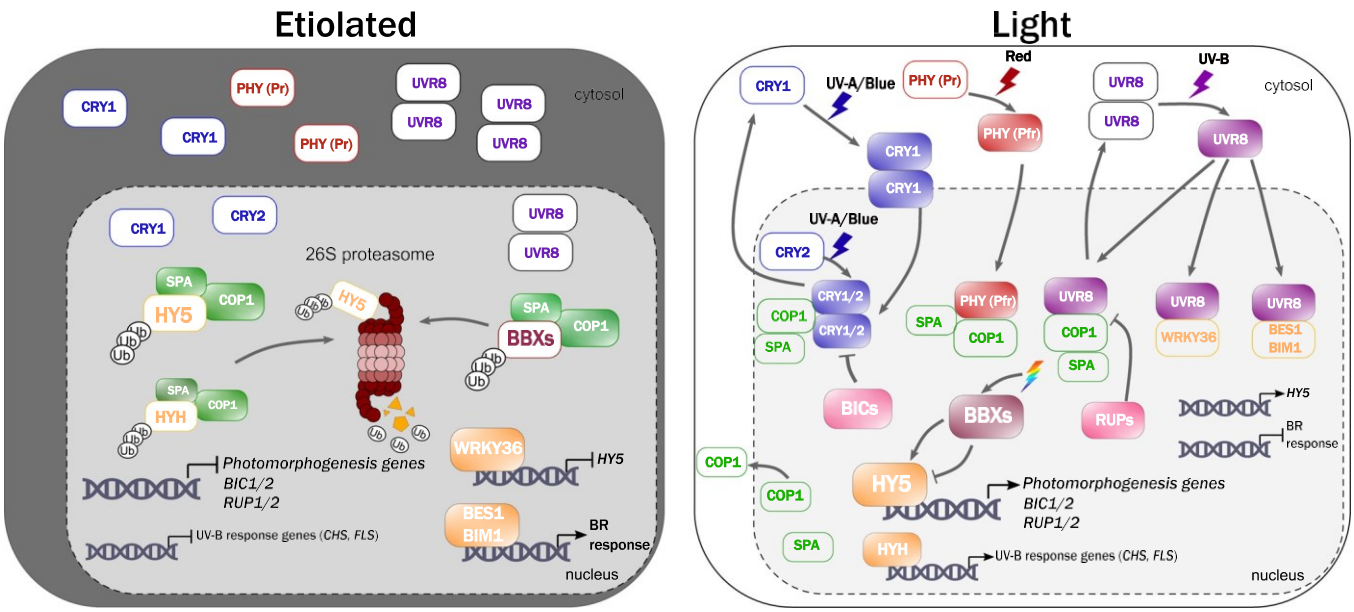

FIGURE 1 Multiplex photoreceptor signal transduction and crosstalk. Left: In darkness the photoreceptors occur in their inactive states, either in the cytosol (PHY, CRY1, UVR8) or in the nucleus (CRY1, CRY2, UVR8). In the nucleus, COP1-SPA complexes target important transcription factors including HY5 and HYH to the 26S proteasome for degradation after ubiquitination. The photomorphogenesis regulatory BBX proteins are also inactivated in darkness. Photomorphogenesis-related genes including *BIC1/2* and *RUP1/2* and other UV-B response genesare not transcribed. In the absence of nuclear active UVR8, WRKY36 and BES1 and BIM1 are active. WRKY36 blocks *HY5* transcription, whileBES1 and BIM1 lead to transcription of BR response genes. Right: Upon light exposure, photoreceptors are activated by their respective wavelengths, leading to conformational changes (PHY), homodimerization (CRY1 and CRY2), or monomerization (UVR8). Additionally, whereassome photoreceptors already reside in the nucleus, others are translocated after photoactivation. The active photoreceptors compete for binding to COP1, allowing COP1 targets to be active. Meanwhile COP1 is shuttled out of the nucleus. BBX proteins are also activated by lightand affect HY5 activity. Simultaneously, UVR8 inactivates WRKY36 and BES1 and BIM1 preventing their

function. Together, this leads to transcription of photomorphogenesis related genes. *BICs* and *RUPs* act within feedback loops, preventing overactivity of CRY and UVR8 signalling, respectively. The membrane-bound phototropins are omitted in this figure given that they exhibit COP1-independent signalling. BBX,B-BOX PROTEIN; BES1, BRI1-EMS1-SUPPRESSOR 1; BIC, BLUE-LIGHT INHIBITOR OF CRYPTOCHROMES; BIM1, BES1-INTERACTING MYC-LIKE1; BR, brassinosteroid; CHS, CHALCONE SYNTHASE; COP1, CONSTITUTIVE PHOTOMORPHOGENIC 1; CRY, cryptochrome; FLS,FLAVONOL SYNTHASE; HY5, ELONGATED HYPOCOTYL 5; HYH, HY5 HOMOLOG; PHY, phytochrome; RUP1, REPRESSOR OF UV-B PHOTOMORPHOGENESIS 1; SPA1, SUPPRESSOR OF PHYA-105 1; Ub, ubiquitin; UVR8, UV RESISTANCE LOCUS 8; WRKY36, WRKY DNA-BINDING PROTEIN 36.

not tagged for proteasomal degradation, accumulate, and initiate transcription of UV-B photomorphogenesis genes (Binkert et al., 2014; Osterlund et al., 2000). Among the latter, *REPRESSOR OF UV-B PHOTOMORPHOGENESIS 1* (*RUP1*) and *RUP2* are transcriptionally activated and act as suppressors of the UV-B response, as part of a negative feedback-loop, through their direct interaction with UVR8(Gruber et al., 2010). This leads to UVR8 re-dimerisation, dampening the UV-B response (Heijde and Ulm, 2013; Wang et al., 2023).

Photoreceptor pathways are intertwined, sharing a certaindegree of overlap at multiple levels. For instance, it has been demonstrated that the absorption spectra of chromophores overlap. The blue light photoreceptors cryptochromes (CRY1/CRY2; Ahmad et al., 2002) and phototropins (PHOT1/PHOT2; Christie & Briggs, 2001; Okajima et al., 2011; Vandenbussche et al., 2014) canrespond to UV-B light. For more detailed information on PHOT and CRY photoreceptor signalling pathways, we refer to the following excellent reviews (Hart & Gardner, 2021; Liscum et al., 2020;Wang and Lin, 2020). Additionally, within the downstream signallingpathways, cross-talk also exists. For example, the COP1-HY5 regulatory module represents a key hub in UVR8, CRY, and phytochrome (PHY) signalling pathways (Figure 1; Cheng et al., 2021; Fraser et al., 2016; Podolec and Ulm, 2018; Ponnu and Hoecker, 2021; Ponnu, 2020). Regardless of these commonalities, plants retain these different photoreceptor pathways. Thus, are plants able to discriminate between different light stimuli or are the huge overlapbetween absorption spectra as well as the downstream signalling responses merely a way to evoke an fine-tuned molecular responseat different depths of light penetration? For instance, most light signalling pathways, inhibit hypocotyl elongation using similar molecular players (Favero et al., 2021). However, UVR8 signalling also depends on the action of WRKY36, independently of other photoreceptors (Yang et al., 2018). Additionally, when treating plants with monochromatic light, different physiological responses can occur. For example, studying the effects of red versus blue light intomato seedlings, it was found that blue light stimulated photo- synthetic capacity, whereas red light increased biomass (Izzo et al., 2020). When comparing the effects of UV-B, UV-A and blue light in *Arabidopsis* plants, a huge number of DEGs were unique for a specific treatment (Rai et al., 2020), hinting at distinct transcriptome responses, alongside others in overlap with one or more other lightsignalling outputs. Together, these findings support the contentionthat photoreceptor signalling pathways are intertwined, whilst eachpathway has its own role to play.

To fully understand the biological function of UV-B sensing in plants from an ecological viewpoint, it is critical to understand if and how signal specificity occurs downstream of perception and whether photoreceptor cross-regulation can act to balance light responses in different environmental and developmental contexts. Here, wedemonstrate that UVR8 signalling is an important part of photo- morphogenesis within a polychromatic environment. However, we argue that the role of UVR8 signalling—in view of other photo- receptor pathways—depends on the developmental stage and the environmental context. Moreover, as shown for the majority of phytohormones (Fàbregas et al., 2018; Savaldi-Goldstein et al., 2007; Vaseva et al., 2018), UV-B signalling as well as other photoreceptorpathways are highly regulated in a spatial manner. For a complete understanding of photoreceptor pathways, there is a need to studyhow the multitude of light signals is perceived in specific cell-types and how this activates specific signalling cascades. Additionally, proper signal cross-talk and intercellular communication is crucial for a harmonised response among the whole plant body.

2 | UV-B SENSING FROM SEEDLING TOFLOWERING: AN ARRAY OF PHOTORECEPTOR PATHWAYS

In natural conditions, plants are exposed to a blend of wavelengths.However, the relative importance of each photoreceptor pathway appears to vary throughout the lifecycle. These variations cannot be explained by differential gene expression of the respective photo- receptors (Vanhaelewyn et al., 2019a). Thus, individual photo-receptor signalling and responses likely depend on a combination offactors, including the exposed organ, the developmental stage, theintensity, spectral properties, and direction of incoming light, as well as the photoperiod. In addition, photoresponses are often linked tothe ecological context. In other words, the relative importance of the different photoreceptor signalling pathways depends on both by thelight quantity and quality that reaches the plant at a given momentduring its life cycle. Secondly, photoresponses are affected by external factors including meteorological and seasonal changes or neighbouring plants, amongst others.

For instance, etiolated seedlings exposed to unilateral mono- chromatic UV-B light display typical phototropic bending. Genetic dissection of photoreceptor pathways revealed that both PHOT- and UVR8-mediated signalling pathways are relevant for bending towards UV-B light (Vanhaelewyn et al., 2016b). However, the importance ofeach photoreceptor appears to depend on timing and dose, with PHOT-dependent bending being crucial during the early response, whereas UVR8 signalling is required only after 2 h. Furthermore, atlow UV-B fluence rates PHOT signalling has a key role, as evidencedby the absence of bending in *phot1phot2* mutants. These findings hint at the biological roles of both PHOT and UVR8 receptors at the etiolated stage of development. We hypothesise that, during the transition of skoto- to photomorphogenesis, the role of UVR8 signalling could be more peripheral, compared to other photo- receptor pathways. The spectral quality of sunlight that

penetratessoils is highly variable: longer wavelengths (e.g., blue) reach deepercompared to shorter wavelengths (e.g., UV-B; Tester and Morris, 1987). Hence, in the pursuit of light, photoreceptor responses are likely balanced, dose- and duration-dependent, with the blue light photoreceptor machinery possibly acting earlier than the UV-Bpathway. In this way, apart from phototropic bending, other PHOT-dependent responses such as blue light-dependent stomatal opening and chloroplast movement are initiated (Gotoh et al., 2018; Kong et al., 2013; Takemiya et al., 2013). In addition, given that PHOT

signalling acts through a phosphorylation cascade (Haga et al., 2015;Takemiya et al., 2013), signalling responses are relatively fast, whereas UVR8 but also the other blue light receptors, CRYs, dependon transcriptional changes, which occur over a longer time (e.g., half an hour to hours instead of minutes). CRYs are also important for other aspects of light-regulated plant development, including cotyle- don expansion, inhibition of hypocotyl elongation, stimulation of stomatal development, amongst others (Wang & Lin, 2020). Hence,upon longer exposure to blue light and with higher intensity, CRYs probably gain importance. When seedlings finally emerge, they are exposed to direct sunlight with longer and intensified exposure to UV-B, activating UVR8-dependent responses. In this context, the regulation of UVR8 mono-/dimerisation is important. Vanhaelewyn et al. (2016b) showed that the RUP-mediated negative feedback loopis essential to keep the UVR8 pathway in check and allow proper PHOT-mediated bending and orientation of etiolated seedlings towards incoming light. Further studies should reveal whether this role for RUP1/2 can be generalised. Interestingly, CRY1/CRY2- mediated signalling under blue light also affected UVR8 activity in a RUP1/2-dependent manner (Tissot & Ulm, 2020), further highlighting intense photoreceptor crosstalk in polychromatic environments. However, a certain degree of caution is warranted. Though these findings hold true for laboratory conditions, it will be interesting to see whether the same mechanisms exist in natural conditions. In addition, most studies regarding the effects of light on etiolated seedlings were performed in *Arabidopsis*. Thus, unravelling the role of UVR8 signalling in other species will shed further light on the biological role of UV-B in natural conditions.

After emerging, seedlings de-etiolate and need to adapt to a multitude of environmental cues. Incoming light induces photo- morphogenic growth, survival strategies and defence mechanisms. As for other photoreceptors, the UVR8-dependent pathway induces plentiful of genes, leading to responses which are overlapping with other light signalling outputs. Once seedlings are actively exposed to natural light, containing the full spectrum, the UV-B sensing machinery becomes more important. Several lines of evidencehighlight the ecological significance of UV-B signalling. UV-B radiation can act as a signal to detect sunlight in low R:FR conditions with high levels of neighbour competition or in dense canopies, by suppressing shade avoidance responses (Hayes et al., 2014; Moriconi et al., 2018). Secondly, UV-B sensing plays a particularly important role during reproduction. Noteworthy, UV-B signalling was discovered to participate in the regulation of photoperiodic flowering, which is crucial for reproductive success. PHYA and CRY2 are considered to be pivotal day length sensors (Mockler et al., 2003). Specifically, CRY2 is vital for the photo- periodic initiation of flowering and acts through a combination of transcriptional and posttranslational mechanisms to control the circadian clock component CONSTANS (CO) (Liu et al., 2008, 2018; Zuo et al., 2011). Most photoreceptor pathways impinge on CO to coordinate optimal flowering time, often with overlapping activities (Takagi et al., 2023). A specific role for UV-B was found in the regulation of photoperiodic flowering (Arongaus et al., 2018). The

authors demonstrated that, under noninductive short-day (SD) conditions, flowering is suppressed by UV-B supplementation. This response depends specifically on RUP2 suppression of CO through a direct interaction that prevents the transcription of *FLOWERING LOCUS T*, a positive regulator of flowering. Interestingly, Arongaus et al. (2018) further demonstrated the existence of a UVR8- dependent pathway that promotes flowering under noninductive SD conditions and is normally suppressed by RUP2. The UV-B/ UVR8 specific pathway which involves RUP2 is probably part of the broader photoreceptor signalling network that regulates and coordinates flowering time. Hence, future work should focus on investigating possible crosstalk with other signalling components, preferably under natural conditions (e.g., simulated sunlight). Apart from bearing the reproductive organs, inflorescence stems also are capable of bending towards unilateral light sources. The bending ofinflorescence stems towards UV-B light is controlled by UVR8-, rather than PHOT-dependent signalling (Vanhaelewyn et al., 2019a). Additionally, in many species, the fraction of UV-B light within sunlight steers certain morphological and physiological changes to increase reproductive success, including flower reorientation, floral pigmentation and synthesis of floral volatiles (Amarasingheet al., 2015; Falara et al., 2013; Khoo et al., 2017; Serrano et al., 2018, 2021). In conclusion, UV-B radiation appears to actas an environmental cue that helps plants to detect gaps in the canopy and increase their photosynthetic output, while it also improves reproductive success and prevents future UV-damage (Mazza & Ballaré, 2015).

In conditions with natural sunlight, photoreceptor pathways alsointertwine. Although UV-B and blue light signals, through UVR8 andPHOT pathways, are considered to be the major inducers of phototropism, at high intensities of blue light (>50 μmol m^{-2} s^{-1}) CRYs appear to take full control. In addition, in response to natural sunlight, CRYs are the major inducers of inflorescence bending (Serrano et al., 2021). Further crosstalk between UVR8 and CRY signalling at the molecular level in *Arabidopsis* seedlings grown in simulated sunlight was demonstrated as well (Rai et al., 2019). CRYsnegatively regulate UVR8 signalling in natural light, either by enhancing the expression of negative regulators of either pathway (Tissot & Ulm, 2020) or by competing for shared signalling components such as COP1. Given that COP1 is required for nuclear retention of UVR8, hijacking of COP1 by CRY could alter UVR8 signalling. These findings emphasise the existence of photoreceptor interplay and the importance of the overlapping part of the CRY1 and UVR8 pathways in outdoor conditions, namely the COP1-HY5 signalling hub. In addition, the role of UV-A as an important part ofnatural sunlight cannot be overlooked. Though initially only PHOTs were considered to be *bona fide* UV-A receptors, recent evidence demonstrated that both CRYs and UVR8 can also respond to UV-A light (Brelsford et al., 2019;

Rai et al., 2020). Shorter wavelengths (<350 nm) required UVR8, whereas longer wavelengths were mediated by CRYs (Rai et al., 2020). Hence, most photoreceptor pathways are activated—in part—by the UV-A component in naturalconditions. Although there is some evidence for UV-A effects in plants (Qian et al., 2021; Vanhaelewyn et al., 2020), including altered biomass and induction of phenolic compounds, additional studies onthe role of UV-A signalling and responses in plants are required.

It is clear that multiple regulatory nodes between CRY, UVR8 and even PHY signalling exist (Tissot & Ulm, 2020) and that this crosstalkis required to balance light responses in natural environments.

3 | COORDINATION OF MULTIPLE SIGNALS BY KEY SIGNALLING HUBS

At the center of UVR8, CRY and PHY signalling, key signalling hubs coordinate downstream responses. COP1-HY5 regulation representssuch an integration node. However, how this signalling hub effectively leads to differentiated downstream responses remains unclear. It has been demonstrated that UVR8, CRY and PHY photoreceptors compete for binding with COP, allowing HY5 to activate downstream transcription (Lau et al., 2019). Upstream of COP1, there are different entries to generate a distinct photo- response. For instance, photoreceptor pathways can influence one another through reciprocal stimulatory or inhibitory feedback mechanisms, as previously demonstrated for UVR8, CRY1/2 and PHYA (Tissot & Ulm, 2020). These feedback loops can affect the photo-equilibrium of UVR8 and CRY1/2 photoreceptors and influ- ence downstream binding to COP1.

HY5 is the key transcription factor of most photoreceptorpathways. Unravelling HY5 transcriptional targets in different lightregimes should thus elucidate the differential impact of specific light signalling pathways. In addition, HY5 activity often depends on heterodimerization with other transcription factors (Gangappa et al., 2013; Singh et al., 2012). Therefore, it is plausible that interactions with specific protein partners is photoreceptor- dependent. B-box domain proteins (BBXs) form another group of pivotal regulatory proteins for photomorphogenic responses (re- viewed in Cao et al., 2023). Certain members of the BBX protein family such as BBX31 have been demonstrated to act as positive regulators of UV-B signalling while they are negative regulators of photomorphogenesis under white light (Yadav et al., 2019). Furtherstudy of the HY5 interactome under specific light conditions, through
f.i. affinity proteomics, could aid in the elucidation of light responses. Interestingly, in seedlings, HY5 is sufficient for UV-B-mediated phototropism (Vandenbussche et al., 2014), whereas in inflorescence stems, redundancy between HY5 and its homolog HYH was found, highlighting specific roles for these transcription factors under certain conditions.

Lastly, several molecular players have been found to be activated by UVR8, though being independent of COP and/or HY5. For instance, the induction of the circadian clock gene *PSEUDO RESPONSE REGULATOR9* (*PRR9*) is HY5-independent
(Bernula et al., 2017), pointing to multiple UVR8 signalling branches. Crosstalk between UVR8 signalling and PHYTOCHROME INTER- ACTING FACTORs (PIFs), transcription factors that act as negative regulators of photomorphogenesis, has also been demonstrated
(Sharma et al., 2019; Tavridou et al., 2020). UVR8 can lower the abundance of PIF4 and PIF5 via their enhanced degradation in a COP1-dependent manner. This mechanism is, in part, responsible of the inhibition of stem and hypocotyl elongation in response to UV-B light. In the regulation of hypocotyl elongation, genetic and molecular analyses have also shown that UVR8 can inhibit the activity of other TFs, including WRKY36, an inhibitor of HY5 transcription in white light, and brassinosteroid-related TFs (Figure 1; Liang et al., 2018; Yang et al., 2018). Other UVR8- specific signalling routes or partners likely exist and could further drive UV-B responses. However, it is clear that UVR8 signalling is part of a multi-orchestrated photomorphogenic response where distinct and shared molecular players play vital roles. As an additional level of regulation, the spatial control of each photo- receptor pathway contributes to its specificity and complexity of cross-talk.

In conclusion, the dynamic regulation of the photo-response atthe molecular level can be understood as follows: depending on thespecific light spectrum, photoreceptors are each activated to a different degree, leading to the activation and/or inhibition of protein accumulation of individual signalling components. Competition for interaction with signalling hubs such as HY5 or COP1 ultimately leadto a net response that is spectrum-specific.

4 | TOWARDS A CELL- TYPE SPECIFIC UNDERSTANDING OF UV-B SIGNALLING

In the last two decades it has become increasingly evident that mostmolecular pathways have distinct *in planta* sites of action to influencegrowth and metabolism. Steering growth plasticity in a dynamic polychromatic environment relies on the transduction of light signals ina spatio-temporal context. This depends on a tight balance between tissue and cell-type specificity of light perception, photoreceptor action and downstream responses that often include hormonal regulation. Cell-type specific interference of major hormones has identified their site of action, which resulted in a fundamental mind-switch on the interpretation of hormone physiology and interactions(Fàbregas et al., 2018; Savaldi-Goldstein et al., 2007; Vaseva et al., 2018). Similarly, photoreceptor signalling is regulated in boththime and space and is probably one of the main drivers of specificity inlight responses. Cell-type specificity is particularly relevant in relationto the observed light gradients within plant tissues. High energy UV will penetrate less profoundly than lower energy wavelengths, such as blue and red light (Gao et al., 2010). In spinach leaves, UV-B is absorbed by epidermal cells (10 μm) owing to their UV screeningpigments, while blue and red light can penetrate to the mesophyll cells (Qi et al., 2003; Vogelmann, 1993). Furthermore, phototropic responses depend on differential photoreceptor signalling betweenilluminated and shaded

sides. It is likely that—depending on the conditions and developmental context—photoreceptor pathways have distinct sites of action, but also depend on intricate cell-to-cell communication through specific molecular players.

Cell-type specific action of certain photoreceptor pathways has been demonstrated previously through expression analyses, the study of reporter lines, and via the analysis of transgenic lines in which photoreceptor-related proteins are under the control of cell- type specific promoters. For instance, phototropic bending towards blue light in etiolated seedlings is mediated by PHOT1 signalling in the upper hypocotyl (Preuten et al., 2013). Moreover, local activation in either epidermal, cortical or endodermal cells can efficiently activate a bending response in the complete seedling (Figure 2). Downstream of PHOT, auxin signalling in the outer layers of the shaded side (e.g., epidermis) drives elongation. In contrast, sensing ofunilateral blue light in monocots occurs in the apical part of the coleoptile, while bending happens in the zone below the apex (Yamamoto et al., 2014). Hence, it is clear that different steps within the signalling cascades can occur in different cell-types and rely on communication between them.

Parallel with the elucidation of the molecular basis of UVR8 signalling, the spatial characteristics of UV-B signalling are being unravelled. Reporter genes in different cell-type and tissue specific

promotor combinations indicated that UV-B signalling is restricted to plant organs directly exposed to UV-B (Vanhaelewyn et al., 2019b). Moreover, opposed to what is reported in seedlings for white light conditions (Chen et al., 2016), there is no HY5, nor HYH protein transfer from shoot to root, indicating that there is no obvious transfer of early UVR8 signalling factors to the roots whatsoever (Vanhaelewyn et al., 2019b). This also holds true at the microlevel: tissues require direct UV-B exposure to activate UVR8 signalling and subsequent induction of HY5 and HYH is tissue-autonomous (Vanhaelewyn et al., 2019a, 2019b). For instance, UV-B supplemen-tation treatments of transgenic lines expressing YFP-UVR8 under thecontrol of cell-type specific promoters (in *uvr8* mutant background)indicated that epidermal UVR8 signalling is sufficient for cotyledon expansion. A role for the epidermal cell layers was also found in the regulation of hypocotyl growth inhibition and phototropic bending ofinflorescence stems (Figure 2; Vanhaelewyn et al., 2019a, 2019b).

It is clear that UVR8 signalling appears to be mostly restricted to the outer cell layers, consistent with the level of UV-B penetration within these particular tissues. Downstream signalling

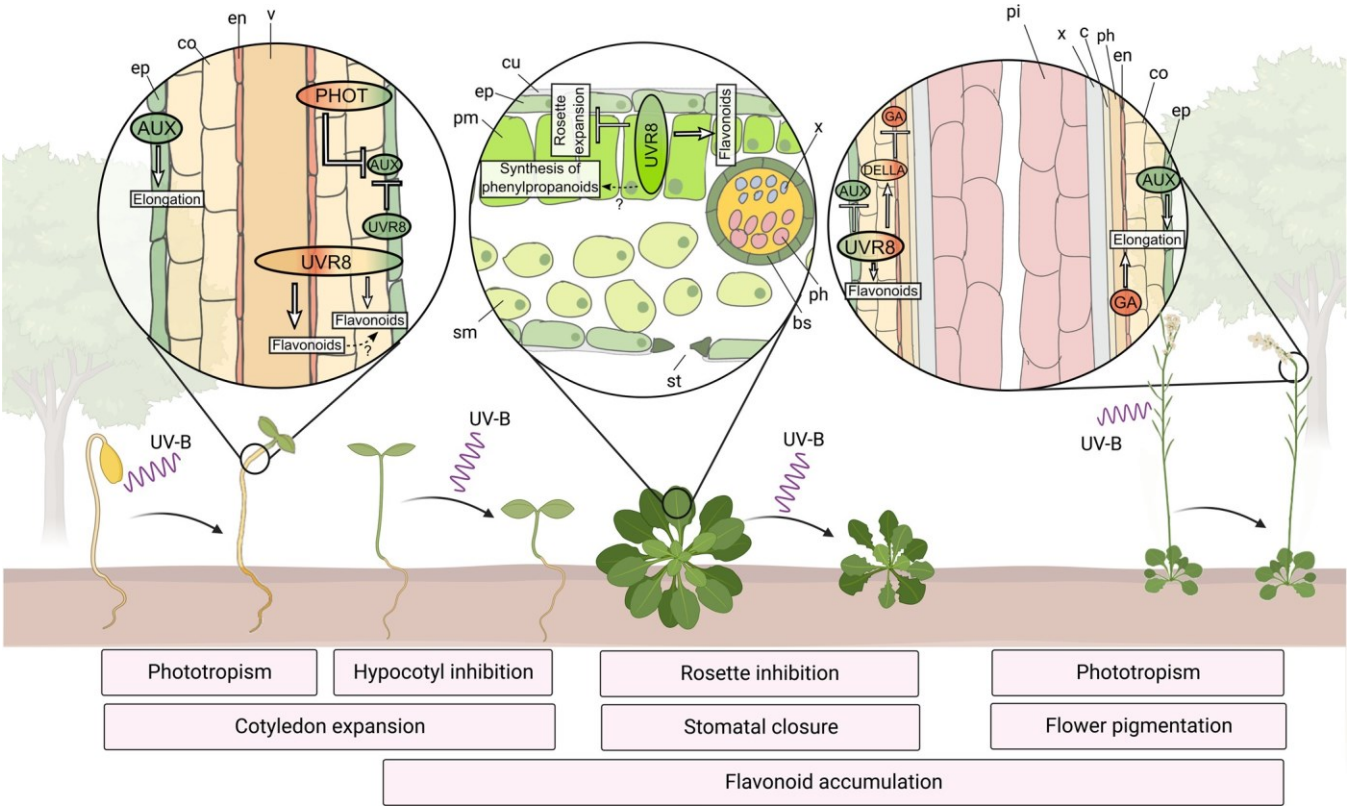

FIGURE 2 Overview of the spatial regulation of photomorphogenic responses regulated by UV-B irradiation. Upon UV-B irradiation plants undergo a series of morphological and metabolic changes as part of the photomorphogenic programme, regulated by photoreceptor and hormonal pathways. Insets show the signal transduction in a cell-type specific manner after unilateral UV-B light in etiolated seedlings (left), UV-B irradiation of rosettes (center), and after unilateral UV-B light in inflorescence stems (right). The colours of the different molecular playerscorrespond with their site of action. Multiple colours represent the protein or hormone being active in more than one cell-type. Arrow-headedlines represent stimulatory effects, while bar-headed lines represent inhibitory effects. Dashed arrows indicate unknown processes. AUX, auxin;bs, bundle sheath; c, cambium; co, cortex; cu, cuticle; ep, epidermis; en, endodermis; GA, gibberellin; ph, phloem; PHOT, phototropin; pi, pith;pm, palisade mesophyll;

sm, spongy mesophyll; st, stoma; UVR8, UVB-RESISTANCE 8; v, vasculature; x, xylem. Image partially created in Biorender. [Color figure can be viewed at wileyonlinelibrary.com]

factors, especially those related to growth, including hormones, are also often active in the outer cell layers (Fàbregas et al., 2018; Procko et al., 2016; Savaldi-Goldstein et al., 2007; Vasevaet al., 2018). The final steps in the UVR8 mediated bending response in etiolated seedlings are caused by a differential auxin response especially in the epidermis, at the opposite sides of the hypocotyl, i.e. on the shaded side compared to the illuminated side (Figure 2; Vandenbussche et al., 2014). Although the gradients in root are opposite of those in shoots, this cell-type specificity is reminiscent of what was found for auxin response in roots (Swarup et al., 2007), and linked to ethylene as a fine-tuning controlling factor of expansion in roots and shoot (Vaseva et al., 2018).

While the epidermal layer contributes considerably to the bending response in inflorescence stems, Vanhaelewyn et al. (2019a) found that the best complementation of the *uvr8* mutationfor bending was seen in lines when *UVR8* was expressed in the cortexcells. Together, these outer cell layers are also the sites with the mostUVR8 signalling (HY5 accumulation) and output (flavonoid synthesis), emphasising the role of external tissue layers in growth responses (Cluis et al., 2004; Vaseva et al., 2018). Interestingly, endodermal activation of the UVR8 pathway can also restore bending responses,at least partially (Figure 2; Vanhaelewyn et al., 2019a). The latter points to a role for endodermis in UVR8 signalling. Here, an interesting interplay between hormones with different sites of action has been discovered. In inflorescence stems, the bending response is linked with auxin and gibberellin (GA) gradients. UV-B irradiation induces an auxin gradient in the stems with an elevated ratio of auxin on the shaded side of the stem compared to the illuminated side. This differential auxin distribution in outer layers allows growth at the shaded side, resulting in bending. This gradient is opposite of what isobserved for HY5, which is known to promote the expression of negative regulators of auxin signalling at the irradiated side of the stem (Lee and Cho, 2006; Zourelidou et al., 2014). Different from auxins, GAs are believed to affect growth in the endodermis (Shani et al., 2013; Ubeda-Tomás et al., 2009). The UVR8-dependent stabilisation of DELLA proteins, negative regulators of GA signalling, in endodermis and cortex of the irradiated side indicates an impingement of light on the central DELLA growth-controlling proteins. GA inactivation genes *GA2OX1* and *GA2OX8* are bothupregulated by UVR8 and are likely direct HY5 targets (Leeet al., 2007; Vanhaelewyn et al., 2019a). It is conceivable that HY5 activation by UVR8 coordinates growth and bending through a harmonised response in multiple cell-layers, with GA inactivation inendodermis and auxin depletion in the outer layers (Figure 2). The spatial characteristics of hormonal crosstalk during phototropic bending would make a worthy topic for future research which could serve as a paradigm for the regulation of other UV-B responses.

The spatial properties of other UV-B effects are, however, lesswell-known. Wild-type plants have a strong upregulated flavonol biosynthesis when exposed to UV-B (Stracke et al., 2010). In young seedlings, the epidermis and mesophyll tissues are especially important for UVR8-mediated pigment synthesis in the cotyledons (Bernula et al., 2017). In the upper hypocotyl region, there also is a

clear UVR8-dependent accumulation of flavonoids in the epidermal cell layer (Vanhaelewyn et al., 2019b). Nevertheless, activation of UVR8 signalling in endodermis and vasculature in a *uvr8* mutant background can also lead to local accumulation of flavonoids upon UV-B exposure. This raises the question as to what role the inner layers could have in UV-B responses. It is tempting to consider thatflavonoids accumulate in the deeper tissues during the early exposure to UV-B light, and are being transported to the outer layers during the acclimatisation period (Figure 2).

The cell-type specific signalling of photoreceptor pathways is vital for a coordinated response to the complex light stimuli to which plants are constantly exposed. Though we are beginning to understand how each cell type, tissue and organ contributes to a harmonised response, there is still a long way to go to fully map themolecular pathways of photomorphogenesis. Fortunately, technolog- ical advances will allow us to study these responses with high resolution. For instance, single-cell transcriptomics has improved our understanding of the production of UV-B screening pigments in leafcells (Procko et al., 2022). The authors demonstrated that palisademesophyll cells are crucial for the synthesis of the phenylpropanoid sinapoylmalate, a cell-type of which the specific molecular function compared to other photosynthetic cells is largely undescribed (Figure 2). Moreover, in silico analysis of the expression of importantlight signalling players in root tissues has revealed that UVR8 is mostly expressed in phloem-related cells and in the mature endodermis (Stafen et al., 2022). To further explore the expression of photoreceptor signalling genes, we have mapped the expression of photosignaling components in a heatmap derived from a shoot apical meristem and leaf cell expression atlas (Zhang et al., 2021). Cell-typesthat are physically close (e.g., epidermis and guard cells, or vascular and companion cells) clustered more together (Figure S1A). Addition- ally, many photoreceptor signalling genes revealed distinct expres- sion patterns, with certain genes (e.g., UVR8) being highly expressedin only few cell-types, whereas others displayed broader expressionpatterns (e.g. *CRY1/2, COP10, DET1, PHYD*; Figure S1A). However, when comparing levels within a given cell-type (i.e., expression changes of all genes relative to each other within a given cell-type),most photoreceptor pathway genes displayed much lower expression than previously reported cell-type marker genes (Zhang et al., 2021), though several photoreceptor components still showed reasonable expression levels (Figure S1B). Nevertheless, when leaving out the marker genes, certain patterns became more visible (Figure 3). Fully coordinated expression of components within a photoreceptor pathway, in which all members are expressed in the same cell types, did not seem to occur. However, taking into account both within-gene (Figure S1B) and within-cell-type comparisons (Figure 3), other interesting patterns were revealed by the in silico analysis. For instance, few genes were characterised by high expression levels, namely *UVR8* (high in epidermis and shoot meristem cells), *PHOT1/2* (both high in most cell-types, but maximum in endodermis and mesophyll for *PHOT1* versus guard cells for *PHOT2*), and *PHYA* (relatively broad expression pattern, but maximum in companion cells). Interestingly, *UVR8* was not

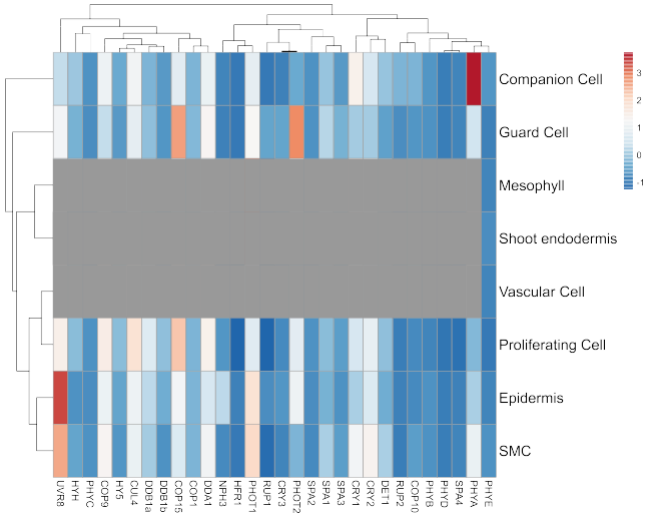

FIGURE 3 Spatial expression of photoreceptor signalling components in *Arabidopsis* shoots. Heat map of average expressionof photomorphogenesis-related genes based on single-cell transcriptomics data from *Arabidopsis* 7- and 14-day-old shoot apical meristems and 3rd leaves of 18-day-old plants grown on soilat 21°C (day)/19°C (night) in long days (16 h light/8 h dark, with a light intensity of 80 μmol/m^2 s using Philips TLD 36W/865 and 36W/830 bulbs; Zhang et al., 2021). Colours indicate relative changes in expression per gene. Columns represent different cell types in shoots and each row is representative for a photoreceptorsignalling component. Analysis and visualisation were done in ClustVis (Metsalu & Vilo, 2015) using default settings and data fromthe Wang lab (Zhang et al., 2021; public database http://wanglab. sippe.ac.cn/shootatlas/). For data pre-processing and standardisation, data were mean-centred around rows (each row was transformed resulting in a mean equal to 0) and unit variance scaling was applied. Both rows and columns are clustered using correlation distance and average linkage. Violin plots and UMAP plots for each gene can be found in Figure S2. ATML1,*ARABIDOPSIS THALIANA* MERISTEM LAYER 1; COP1, CONSTITUTIVE PHOTOMORPHOGENIC 1; CRY, cryptochrome;CUL4, CULLIN4; CYCA1;1, CYCLIN A1;1; DDA1, DDB1-ASSOCIATED 1; DDB, DAMAGED DNA BINDING PROTEIN; DET1, DE-ETIOLATED 1; FBA5, FRUCTOSE-BIPHOSPHATE ALDOLASE 5; GDU4, GLUTAMIN DUMPER 4; HFR1, LONG HYPOCOTYL IN FAR-RED1; HY5, ELONGATED HYPOCOTYL5; HYH, HY5 HOMOLOG; KNAT1, KNOTTED-LIKE FROM *ARABIDOPSIS THALIANA*; MYB60, MYB DOMAIN PROTEIN 60; NPH3, NON-PHOTOTROPIC HYPOCOTYL 3; PHOT, PHOTOTROPIN; PHY,PHYTOCHROME; RUP, REPRESSOR OF UV-B PHOTOMORPHOGENESIS; SMC, shoot meristematic cells; SPA,SUPPRESSOR OF PHYA-105; SUC2, *ARABIDOPSIS THALIANA* SUCROSE-PROTON SYMPORTER2; UVR8, UV-B-RESISTANCE 8.
[Color figure can be viewed at wileyonlinelibrary.com]

limited to the outer layers, but also extended into the endodermis and vascular tissues. As proposed for phototropic bending of inflorescence stems (Vanhaelewyn et al., 2019a)—and in contrastto general belief—the inner tissues probably contribute to UVR8- mediated responses, in addition to the outer layers. Crosstalk with the flowering initiation pathway through CO and FT, which are most active in phloem companion cells, could occur at this location (Arongaus et al., 2018). Though relatively low, *RUP2* was also expressed in companion cells and other vasculature cells, whereas *RUP1* was mostly restricted to the epidermis, guard cells and endodermis. *CRY1/2* revealed lower expression compared to *UVR8* and *PHOTs*, but was more widespread, whereas expression for*CRY3* was mostly absent. In contrast to *PHYA*, none of the other phytochromes had considerable expression. Most members of the COP1-SPA-HY5 molecular hub were low expressed, though present in the majority of cell types. However, other proteins involved in the E3 ligase complex (e.g., *CUL4*, *DET1*, *DDB1a*) or the COP9 signalosome (e.g., *COP9*, *COP15*/*FUS5*) showed higher expression and in more cell-types. These findings suggest that the latter could be more prone to transcriptional regulation. Together, these findings support that photoreceptor signalling components can have cell-type specific expression patterns which are likely related with their function. Further validation through targeted inactivation of relevant genes will shed light on their proposed function. Moreover, such analyses do not consider posttranscriptional effects on the accumulation of certain photo- receptor signalling components, nor do they take into account protein transport or intercellular communication.

5 | CONCLUSIONS AND FUTUREPERSPECTIVES

To understand the development of plants growing in natural environments as well as those cultivated for agricultural purposes, it is crucial to unveil the molecular pathway underlying UV-B perception, including its interactions with other photoreceptor pathways. The field of photobiology is constantly evolving with new insights into plant responses to dynamic and polychromatic environments and with the discovery of novel molecular playersand crosstalk mechanisms. Future studies should focus on the spatial and temporal regulation of UV-B responses. We are convinced that novel techniques such as single-cell transcrip- tomics will greatly benefit the current knowledge on transcrip- tional regulation of UVR8 signalling and its interaction with other photoreceptor pathways, albeit requiring well-designed experi-

mental set-ups. In that regard, the light conditions should be carefully controlled to elucidate the function of specific photomorphogenesis-related components. For examples, filters that exclude UV-B, UV-A, or blue light wavelengths in simulated sunlight conditions will help to unravel the spatial control of specific light signalling pathways as well as to understand photoreceptor cross-regulation. Additionally, with rapid advances in imaging mass cytometry (Leroux et al., 2021), mass spectrome- try imaging and even nanotechnology (Clark et al., 2022; Dong et al., 2020; Son et al., 2023), the precise mapping of proteins or metabolites, such as hormones, antioxidants and pigments, is becoming more feasible. It will be exciting to follow-up on future breakthroughs in UV-B research.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in http://wanglab.sippe.ac.cn/shootatlas.

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