Beyond Arabidopsis: Differential UV-B Response Mediated by UVR8 in Diverse Species

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Ultraviolet-B radiation (UV-B, 280–315 nm) is an important environmental signal that regulates growth and development in plants. Two dose-dependent UV-B response pathways were described in plants: a specific one, mediated by UVR8 (the specific UV-B receptor) and an unspecific one, activated by the oxidative damage produced by radiation. The constitutively expressed receptor appears inactive as a dimer, with the two monomers dissociating upon UV-B irradiation. The monomer then interacts with COP1, an ubiquitin ligase, hindering its ability to poly-ubiquitinate transcriptional factor HY5, thus averting its degradation and activating the photomorphogenic response. HY5 induces the synthesis of proteins RUP1 and RUP2, which interact with UVR8, releasing COP1, and inducing the re-dimerization of UVR8. This mechanism has been thoroughly characterized in Arabidopsis, where studies have demonstrated that the UVR8 receptor is key in UV-B response. Although Arabidopsis importance as a model plant many mechanisms described in this species differ in other plants. In this paper, we review the latest information regarding UV-B response mediated by UVR8 in different species, focusing on the differences reported compared to Arabidopsis. For instance, UVR8 is not only induced by UV-B but also by other agents that are expressed differentially in diverse tissues. Also, in some of the species analyzed, proteins with low homology to RUP1 and RUP2 were detected. We also discuss how UVR8 is involved in other developmental and stress processes unrelated to UV-B. We conclude that the receptor is highly versatile, showing differences among species.

Keywords: UV-B, UVR8, RUP1, RUP2, Arabidopsis, terrestrial plants, photomorphogenic response, gene expression
INTRODUCTION

Approximately 7% of all solar radiation that reaches the Earth's surface is ultraviolet light (UV) (Frohnmeyer and Staiger, 2003). UV radiation is divided into three wavelength ranges: UV-A (315–400 nm), UV-B (280–315 nm) and UV-C (100–280 nm) (Björn, 2015). UV-C, the most energetic of the three, is completely absorbed by the ozone (O₃) layer. UV-A is not attenuated by ozone, but it is the least damaging and acts as a photomorphogenic signal (Björn, 1996). Approximately 95% of UV-B radiation is absorbed by the ozone layer and reaches the Earth's surface with an average intensity of 1 W.m⁻² (Cejka et al., 2011). Depending on the dosage, UV-B radiation can either act as a signal or cause damage. Due to its high energy, UV-B can break chemical bonds and produce highly reactive molecules.

The natural dynamic balance of ozone levels was abruptly interrupted by anthropogenic emission of ozone-depleting substances (ODS) (from the 1960's to the end of the 1990's), with a decrease in ozone levels and an increase in UV-B radiation reaching the Earth's surface (Steinbrecht et al., 2018). Thirty years after the Montreal Treaty, which banned ODS emission worldwide, the ozone layer shows signs of recovery (Ball et al., 2018; Steinbrecht et al., 2018). Nonetheless, this recovery has not been reported in the areas where practically all inhabitants and cultivars are located (Chipperfield et al., 2017, Weber et al. (2018). Some papers have even reported a decrease in stratospheric ozone in these latitudes since 1998 (Ball et al., 2018).

The most common effects induced by UV-B radiation in plants are biomass decrease (Tevini and Teramura, 1989; Vandenbussche et al., 2018), alterations in cuticle and epidermis (Tevini and Steinmüller, 1987), abnormal growth (Teramura and Sullivan, 1994; Searles et al., 2001), and damages to photosystems I and II (Pang and Hays, 1991; Liu et al., 2013). These effects can affect both cultivar quality and yield (Bais et al., 2018). It has been estimated that cultivar growth decreases approximately 1% for each 3% increase in UV-B radiation (Ballaré et al., 2011), but this could be more dramatic in UV-B sensitive cultivars (Hakala et al., 2002; Gao et al., 2003; Hidema and Kumagai, 2006; Zhua and Yang, 2015). UV-B radiation could also have effects on food quality, by affecting levels and composition of vitamins, fatty acids, polyphenols, and flavonoids or anthocyanins, thus modifying nutritional and organoleptic characteristics (Choudhary and Agrawal, 2016; Reddy et al., 2016; Tripathi and Agrawal, 2016; Nguyen et al., 2017; Wang et al., 2017; Wu et al., 2017).

Knowing how plants react to UV-B radiation is therefore crucial to establish damage reducing strategies for cultivars. In the past 20 years, there have been great advances in this area, but most of the work has been done using Arabidopsis thaliana as a model plant. One of the outstanding advances has been the characterization of the first specific UV-B photoreceptor: UV RESISTANCE LOCUS 8 (UVR8) (Rizzini et al., 2011; Christie et al., 2012; Wu et al., 2012).

The aim of this article is to review the current documented knowledge concerning plants’ responses to UV-B radiation, venturing beyond the information available for Arabidopsis thaliana and focusing on other species. To achieve this, we spotlighted the responses mediated by the UVR8 receptor and the UV-B response repressors, RUP proteins (REPRESSOR OF UV-B PHOTOMORPHOGENESIS). Furthermore, we analyzed the participation of UVR8 in diverse stresses, fruit development, and UV-B-independent responses.

UVR8-MEDIATED UV-B SIGNALING IN ARABIDOPSIS

Protein UV RESPONSE LOCUS 8 (UVR8) has been characterized as the UV-B radiation receptor (Kliebenstein et al., 2002; Brown et al., 2005; Rizzini et al., 2011; Christie et al., 2012; Jenkins, 2014). As shown in Figure 1, in presence of UV-B, UVR8 changes its quaternary structure from homodimer to active monomer, translocating from the cytoplasm to the nucleus, where it is functional (Kaiserli and Jenkins, 2007; Rizzini et al., 2011; Christie et al., 2012; Qian et al., 2016; Yin et al., 2016). Constitutively photomorphogenic 1 (COP1) is part of the E3 ubiquitin ligase complex, where it interacts with SUPPRESSOR OF PHYA (SPA1), poly-ubiquitinating the transcriptional factors ELOGATED HYPOCHOTYL 5 (HY5) and HY5 HOMOLOG (HYH), which are subsequently degraded via proteasome (Lau and Deng, 2012; Huang et al., 2014). In presence of UV-B radiation, the UVR8 monomer interacts with COP1 and disengages COP1-SPA from the E3 ubiquitin ligase complex, avoiding ubiquitination and subsequent degradation of HY5 and HYH (Favory et al., 2009; Cloix et al., 2012). HY5 levels increase, inducing its own expression and regulating the expression of key genes in UV-B response (Brown et al., 2005; Binkert et al., 2014).

One of the genes induced by HY5 encodes for RUP (REPRESSOR OF UV-B PHOTOMORPHOGENESIS) proteins, which participate in the negative feedback regulation by binding to UVR8 and promoting its re-dimerization (Gruber et al., 2010; Heijde and Ulm, 2013). When plants are grown in diurnal periods, UVR8 reaches a dimer/monomer equilibrium in which RUP proteins are crucial for correct dimerization (Findlay and Jenkins, 2016). Other proteins also participate in the negative feedback regulation of UV-B: SALT TOLERANCE/BBX24 (STO/BBX24), RADICAL-INDUCED CELL DEATH1 (RCD1) and DWD HYPERSENSITIVE TO UV-B 1 (DHU1) (Jiang et al., 2009, 2012a,b; Kim et al., 2017). BBX24 binds to RCD1 and interacts with HY5 and COP1, stabilizing COP1, reducing HY5 accumulation and inhibiting its activity as a transcriptional factor (jiang et al., 2012a). DHU1 sequesters COP1, found in the complex UVR8-COP1, diminishing the UV-B response (Kim et al., 2017).

On the other hand, it has been demonstrated that UVR8 monomers can interact with the transcriptional factors WRKY DNA-BINDING PROTEIN 36 (WRKY36), BRI1-EMS-SUPPRESSOR1 (BES1) and BES1-INTERACTINGMYC-LIKE 1 (BIM1) in the nucleus, as part of a signaling cascade in response to UV-B (Favory et al., 2009; Liang et al., 2018; Yang et al., 2018a). Free WRKY36 binds to the HY5 promoter and blocks its transcription. When UVR8 interacts with
FIGURE 1 | UVR8-mediated signal transduction model in Arabidopsis. In white light (left panel), the UV-B photoreceptor UVR8 homodimer and E3 ubiquitin ligase complex are located in the cytosol. The E3 ubiquitin ligase promotes degradation of the HY5 and HYH transcription factors. HY5, acting redundantly with HYH, mediates transcriptional responses. Transcription factors HY5, WRKY36, BIM1 and the functional BES1 are localized in the nucleus. HY5 binds to its own promoter to activate HY5 transcription, and WRKY36 also binds to the HY5 promoter to inhibit its transcription. BIM1 and BES1 act together to induce the expression of brassinosteroid (BR)-responsive genes. When plants are exposed to UV-B (right panel), the UVR8 homodimer is dissociated into active monomers. Monomeric UVR8 binds to COP1–SPA and elicits the COP1–SPA dissociation from the CUL4–DDB1 E3 ubiquitin ligase complex precluding HY5/HYH degradation. UVR8–COP1–SPA travels to the nucleus and facilitates HY5 protein stabilization and enhances the binding of HY5 to its own promoter. UVR8 monomer interacts with WRKY36 to inhibit WRKY36 binding to the HY5 promoter hence removing the inhibition of HY5 expression. In addition, the UVR8 monomer interacts with BIM1 and the functional dephosphorylated BES1 to inhibit their binding to the BR-induced genes involved in cell elongation, thus repressing the expression of BR-induced elongation genes and further repressing the BR-promoted plant growth. HY5 induces the transcription of key genes in the photomorphogenic response and defense mechanism. RUP1 y RUP2 are two of the genes induced by HY5. RUP proteins (RUP1 and RUP2) negatively regulate UVR8 by binding to the C27 region, displacing COP1, and promoting re-dimerization of the photoreceptor (pink arrows). RUP could act both in the nucleus and in the cytosol. Currently, the mechanism that transports RUP between the cytosol and the nucleus is unknown. The figure is based on the models proposed by Jenkins (2017) and Liang et al. (2019). UV-B, ultraviolet-B radiation; UVR8, UV RESISTANCE LOCUS 8; COP1, CONSTITUTIVELY PHOTO-MORPHOGENIC 1; HY5, ELONGATED HYPOCOTYL 5; HYH, HY5 HOMOLOG; SPA1, SUPPRESSOR OF PHYA; DDB1, DNA DAMAGE-BINDING PROTEIN 1; CUL4, CULLIN 4; WRKY36, WRKY DNA-BINDING PROTEIN 36; BES1, BRI1-EMS-SUPPRESSOR1; BIM1, BES1-INTERACTING MYC-LIKE 1; BRs, Brassinosteroids; RUP1 and RUP2, REPRESSOR OF UV-B PHOTO-MORPHOGENESIS 1 and 2; FLS, FLAVONOL SYNTHASE; UVR3, UV REPAIR DEFECTIVE 3; ELIP1, EARLY LIGHT-INDUCIBLE PROTEIN 1; CHS, CHALCONE SYNTHASE.

WRKY36, this factor is removed and HY5 can induce its expression (Yang et al., 2018a). BES1 and BIM1 are part of the brassinosteroids’ (BRs) signaling cascade (Yin et al., 2005). BES1 interacts with BIM1 and binds to DNA, inducing BRs response genes (Yin et al., 2005; Belkhadir and Jaillais, 2015; Liang et al., 2018). The monomer UVR8 binds preferentially to dephosphorylated BES1, which is the active form, and by precluding its interaction with DNA, promotes one of the
classic responses to UV-B: the inhibition of hypocotyl growth (Vert and Chory, 2006; Jiang et al., 2015; Liang et al., 2018).

**UVR8: FROM GREEN ALGAE TO HIGHER PLANTS**

UVR8 is functional as a receptor because of amino acid sequences that are key for UV-B perception, homodimerization, and COP1 interaction. UV-B perception is achieved through tryptophan residues (O’Hara and Jenkins, 2012; Ulm and Jenkins, 2015). UVR8 monomers have three Gly-Trp-His-Thr motifs (GWRHT) that form a tryptophan triade (W233, W285, and W337), where W285 is the main UV-B sensor. Once the tryptophans absorb UV-B radiation, the dimer dissociates into its monomers (Christie et al., 2012; Wu et al., 2012). The interaction of UVR8 with COP1 may occur either in a UV-B dependent fashion, through a β-propeller domain, or constitutively, via core VP (Val-Pro) in the UVR8C27 domain (Cloix et al., 2012; Yin et al., 2015). By analyzing the amino acid sequences and focusing on the key motifs for UVR8 function, UVR8 sequences have been identified in green algae, bryophytes, lycophytes, and angiosperms (Rizzini et al., 2011; Wu et al., 2012; Fernández et al., 2016). These motifs are highly conserved from green algae to higher plants. At the moment, no UVR8 homologs in gymnosperms have been identified or characterized, making it an issue worth exploring. Characterization studies for the UVR8 receptor have been performed in Arabidopsis (Rizzini et al., 2011; Cloix et al., 2012; Wu et al., 2012), and, in recent years, studies of UVR8 in other species have been undertaken. In green algae, such as *Chlamydomonas reinhardtii* (Cr), CrUVR8 dimers dissociate upon UV-B irradiation and re-form when transferred to white light. Interaction between CrUVR8 and CrCOP1 in *Chlamydomonas* has been confirmed in yeast two-hybrid assays. In addition, CrUVR8 complements the Arabidopsis *uvc8* mutant, indicating that the molecular mechanism of action characterized in Arabidopsis is well-conserved (Tilbrook et al., 2016).

Soriano et al. (2018) studied the structure and function of UVR8 in two bryophytes, the moss *Physcomitrella patens* and the liverwort *Marchantia polymorpha*. Unlike Arabidopsis, which only has one *UVR8* gene, *P. patens* expresses two *UVR8* genes that encode functional proteins, whereas the single *M. polymorpha* *UVR8* gene expresses two transcripts by alternative splicing, and the resulting proteins are functional. In *Physcomitrella*, the UVR8 dimer also dissociates in the presence of UV-B (as in Arabidopsis), but in its absence, both dimers and monomers were detected. However, in *M. polymorpha*, the UVR8 monomer is present independently of UV-B treatment and the dimer UVR8 is barely detected.

UVR8 is translocated from the cytoplasm into the nucleus, where it accumulates rapidly when Arabidopsis plants are exposed to UV-B (Kaiserli and Jenkins, 2007; Yin et al., 2016). Contrary to Arabidopsis, both *M. polymorpha* GFP-UVR8 fusion proteins encoded in *uvc8* are found in the nucleus, independently of UV-B treatment. Nevertheless, both *Marchantia* and *Physcomitrella* UVR8 complement Arabidopsis *uvc8* mutants, thus reinstating HY5 transcript levels, the accumulation of the chalcone-synthase enzyme (CHS), and the suppression of hypocotyl growth in response to UV-B.

In Angiosperms such as *Chrysanthemum morifolium* (Cm), *Populus euphratica* (Pe), and *Malus domestica* (Md), heterologous expression of CmUVR8, PeUVR8, and MdUVR8 rescued the deficient phenotype of *uvc8* mutants in Arabidopsis in response to UV-B. In addition, the CmUVR8-CmCOP1, and MdUVR8-MdCOP1 interactions were confirmed using a yeast two-hybrid assay. PeUVR8-AtCOP1 interaction was verified using bimolecular fluorescence complementation (BiFC) assay (Mao et al., 2015; Zhao et al., 2016; Yang et al., 2018b).

In agreement with previous studies in Arabidopsis, overexpression of UVR8 in *Solanum lycopersicum* (Sl) increased tolerance to UV-B, and gene silencing in tomato lines (SiUVR8Ri) promoted UV-B hypersensitivity (Li H. et al., 2018). UV-B response gene induction, such as *HY5* and *CHS*, as well as anthocyanin accumulation were repressed in SiUVR8Ri, indicating that SiUVR8 plays an essential role in UV-B response. GFP-SiUVR8 proteins expressed in *Nicotiana* showed cytoplasm to nucleus translocation as reported for Arabidopsis (Li H. et al., 2018).

In all the species mentioned, the UVR8 receptor was functional and behaved similarly to the receptor described for Arabidopsis. This confirms the predicted presence of UVR8 in green algae, bryophytes, and angiosperms by bioinformatics analyses. The existence of UVR8 in ancestral organisms, such as green algae, could be related to the elevated UV-B dose in the primitive atmosphere and the ensuing self-protection required by the first photosynthetic plants (Jenkins, 2017).

**UVR8 EXPRESSION IN DIFFERENT PLANT SPECIES**

The expression of the *UVR8* gene in Arabidopsis (AtUVR8) is ubiquitous and constitutive in plant tissues, and this includes roots, which do not receive direct light (Rizzini et al., 2011; Jenkins, 2017). Arabidopsis has only one copy of the *UVR8* gene, while several species contain at least two *UVR8* genes (Brown et al., 2005; Fernández et al., 2016). Although, at the moment, there is no evidence of functional differences between UVR8 proteins within analyzed species, the possession of multiple genes provides the potential for differential expression regulation.

As can be observed in Table 1, in species such as *P. euphratica*, *S. lycopersicum*, *Betula platyphylla*, *C. morifolium*, or *Malus domestica*, the *UVR8* gene is expressed in all the tissues, as in Arabidopsis, but the transcript levels differ significantly between tissues (Mao et al., 2015; Li H. et al., 2018; Yang et al., 2018b). In *Populus*, expression of *PeUVR8* is higher in shoots and leaves, declines in stems, and is weak in roots (Mao et al., 2015). In *Solanum* SIUVR8 expression levels are higher in flowers than in the other tissues analyzed (Li X. et al., 2018). The expression of *BpUVR8* in Betula is highest in leaves and significantly reduced in xylem, phloem, and inflorescences (Li H. et al., 2018). In *Chrysanthemum*, expression is higher in leaves, followed by flowers and weakest in roots. *MdUVR8* gene expression in apple trees is higher in stems, lower in fruits and roots, and very
low in leaves and flowers (Zhao et al., 2016). Besides changes in expression levels among apple tissues, the abundance of the transcript MdUVR8 also varies throughout the development of the fruit (Henry-Kirk et al., 2018). In Vitis vinifera, expression of VvUVR8 in the grape berry varies, and it is four to five times higher in pre-verasion than in post-verasion (Liu et al., 2015).

The receptor’s constitutive presence allows a rapid response to mitigate the damage caused by UV-B (Rizzini et al., 2011). Arabidopsis UVR8 over-expressing mutants are more tolerant and adapt better to UV-B (Favory et al., 2009; Morales et al., 2013). If we assume that higher UVR8 expression correlates with an increase in protein levels, differential expression in the diverse tissues could be associated with different degrees of UV-B tolerance throughout the plant.

AtUVR8 expression levels do not vary significantly in response to UV-B (Kliebenstein et al., 2002; Tohge et al., 2011; Fasano et al., 2014). Similarly, VvUVR8 expression does not change with UV-B treatment in berry skin (Carbonell-Bejerano et al., 2014). Whereas in M. polymorpha and P. patens, UVR8 expression remains constant in presence of UV-B (Soriano et al., 2018), there are some species where UVR8 expression varies significantly in response to UV-B (see Table 2). In birch tree, after 6 h exposure to UV-B, BpUVR8 expression increases 3.5 times with respect to the control, with a maximum peak at 9 h (4.65 times more than in the control) (Li J. et al., 2018). In Antarctic moss Pohlia mutans, expression levels of genes involved in the UV-B signaling pathway, PnUVR8, PnHY5 and PnCOP1, increase significantly after 3 h treatments with UV-B (Li et al., 2019). In another Antarctic species, such as Colobanthus quitensis, the increase in

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### TABLE 1 | UVR8 gene expression in different organs and developmental stages in diverse species.

| Species               | Gene    | Plant Material                  | Type of analysis         | Expression levels in organs/developmental stages (X: times/fold with respect to the tissue with lowest expression) | References |
|-----------------------|---------|---------------------------------|--------------------------|------------------------------------------------------------------------------------------------|------------|
| Arabidopsis thaliana  | AtUVR8  | Plants                          | Analysis in different organs | Present in all organs. No significant expression changes among different organs                                           | Kaiserl and Jenkins, 2007; Rizzini et al., 2011 |
| Betula platyphylla    | BpUVR8  | Trees grown in natural conditions                     | Analysis in different organs | Inflorescence (1x); Xylem (1.5x); Phloem (0.75x); Leaves (6.5x)                                           | Li X. et al., 2018 |
| Chrysanthemum morifolium | CmUVR8 | 8-month-old plants in natural conditions       | Analysis in different organs | Roots (1x); Stems (4.5x); Leaves (6.4x); Flowers (4.5x)                                                      | Yang et al., 2018b |
| Malus domestica       | MdUVR8  | Trees grown in natural conditions              | Analysis in different organs | Root (1x); Stem (15x); Leaf (0.1x); Flower (0.2x); Fruit (5x)                                               | Zhao et al., 2016 |
| Populus euramatica    | PeUVR8  | Trees grown in natural conditions              | Analysis in different organs | Roots (1x); Stems (10x); Leaves (22.5x); Shoots (6.5x); Buds (20x)                                        | Mao et al., 2015 |
| Solanum lycopersicum  | SlUVR8  | Plants grown in outdoor field for 4 months     | Analysis in different organs | Root (1x); Stem (2.8x); Leaf (7.8x); Flower (9x)                                                              | Li X. et al., 2018 |
| Vitis vinifera        | VvUVR1  | Grapevine organs of field-grown plants         | Analysis in different organs | Seed post veraison (1x); Root (3.7x); Tendril (7.2x); Leaf (5x); Inflorescence (4.5x); Flower (6.3x)       | Loyola et al., 2016 |
| Cucumis sativus       | CsUVR8  | Hypocotyl of two near isogenic lines           | Hypocotyl elongation during the first 15 days of growth             | Significant variations in expression levels during the first 15 days                                         | Bo et al., 2016 |
| Malus x domestica     | MdUVR8  | Apple peel from 35 days to 146 days after full bloom | Apple ripening          | Expression levels change during apple ripening. Expression reaches a maximum 104 days after full bloom   | Henry-Kirk et al., 2018 |
| Solanum lycopersicum  | SlUVR8  | Fruit pericarp of plants grown in outdoor fields | Fruit development and ripening                                | Significant variations in fruit: 20 days post-anthesis (2.4x); breaker fruit (5x); red fruit (3.1 x) | Li H. et al., 2018 |
| Solanum melongena     | SmUVR8  | Peels of eggplants grown in horticultural farm  | Fruit ripening                                       | Expression levels change during fruit ripening. Expression first increases and later is repressed.       | Li H. et al., 2018 |
| Vitis vinifera        | VvUVR1  | Berry skin of field-grown plants              | Vearaison (~4 weeks to +8 weeks) | Expression levels decrease significantly during veraison                                                      | Loyola et al., 2016 |
| Vitis vinifera        | VvUVR1  | Flowers of field-grown plants                | Flower development (~10 weeks before anthesis to anthesis)       | Expression levels decrease significantly during flower maturation, with the lowest values 8 weeks before anthesis | Loyola et al., 2016 |
### TABLE 2 | UVR8 gene expression in different plants treated with UV-B.

| Specie                  | Gene      | UV-B treatment                                                                 | Changes in gene expression                                                                 | Tissue             | References                   |
|-------------------------|-----------|--------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------|-------------------|-------------------------------|
| Arabidopsis thaliana    | AtUVR8    | Plants were grown on compost for 3 weeks under 20 μmol m⁻² s⁻¹ constant white light at 21°C and then treated with 3 μmol m⁻² s⁻¹ UV-B for 4 h | No significant changes                                                                 | Leaf              | Kaiserli and Jenkins, 2007   |
| Arabidopsis thaliana    | AtUVR8    | Plants were grown in vitro for 14 days under white light (100 μmol s⁻¹ m⁻²) supplemented with UV-B (5 μmol m⁻² s⁻¹) for 2 h | No significant changes                                                                 | Complete plant    | Fasano et al., 2014          |
| Arabidopsis thaliana    | AtUVR8    | Plants were grown for 10 days before being irradiated with 0.2 kJ UV-B (m⁻² s⁻¹) or 1.4 kJ m⁻² h⁻¹ unweighted UV-B for 3 d | No significant changes                                                                 | Leaf              | Kleibenstein et al., 2002    |
| Betula platyphylla      | BpUVR8    | Seedling were exposed to 1.5 μmol m⁻² s⁻¹ UV-B during 3, 6, 9, 12 and 24 h. | No significant changes in the 3 h treatment. In the remaining treatments, expression increases: 6 h (5.9x) 9 h (7.9x) 12 h (6.5x) and 24 h (2.7x) | 3-week-old seedling | Li X. et al., 2018            |
| Colobanthus quitensis   | CpUVR8    | Different doses during 24 h: low 1.7 kJ m⁻² d⁻¹, medium 15.8 kJ m⁻² d⁻¹, and high 21.4 kJ m⁻² d⁻¹. | Reach their highest level 3 h after medium treatment (13x) and 6 h after high treatment (16x) | Complete plant    | Contreras et al., 2019       |
| Cucumis sativus         | CsUVR8    | ~0.15 Jm⁻² min⁻¹ UV irradiation treatment started on the third day after germination with 5 h exposure per day. | No significant changes                                                                 | Hypocotyl         | Bo et al., 2016               |
| Maku domestica          | MdUVR8    | Continuous white light (20 μmol m⁻² s⁻¹) supplemented with UV-B (305 nm) (1.5 μmol m⁻² s⁻¹). | Increased progressively and reached a peak at 6 h, but decreased during the next period of time and reached a minimum at 24 h | Fruit skin        | Zhao et al., 2016             |
| Marchantia polymorpha   | MpUVR8    | Plants were grown under continuous 80 μmol m⁻² s⁻¹ white light. Plants were placed in darkness for 16 h and then exposed to either 20 μmol m⁻² s⁻¹ white light or 3 μmol m⁻² s⁻¹ narrowband UV-B for 3 h | No significant changes                                                                 | Complete plant    | Soriano et al., 2018         |
| Marchantia polymorpha   | MpUVR8    | Plants were exposed to different doses of UV-B daily for 12 h: Control: 51 μW cm⁻² UV-B, low-fluence UVB treatments: 124 μW cm⁻² UV-B, | No significant change                                                                 | Complete plant    | Clayton et al., 2018          |
| Phycomitrella patens    | PpUVR8.1  | Plants were in dark 16 h and then exposed to 20 μmol m⁻² s⁻¹ white light or 3 μmol m⁻² s⁻¹ UV-B (312 nm) 30 min | No significant changes                                                                 | Complete plant    | Soriano et al., 2018         |
| Phycomitrella patens    | PpUVR8.2  | Plants were in dark 16 h and then exposed to 20 μmol m⁻² s⁻¹ white light or 3 μmol m⁻² s⁻¹ UV-B (312 nm) 30 min | No significant changes                                                                 | Complete plant    | Soriano et al., 2018         |
| Pohlia nutans           | PnUVR8    | UV-B radiation was 0.20 mW cm⁻² for 3 h or 6 h | PnUVR8 was significantly after 3h treatments with UV-B | Green gametophyte | Li et al., 2019               |
| Prunus persica          | PpUVR8    | Fruits were exposed 10 min to 1.39 kJ m⁻² and 60 min to 8.33 kJ m⁻² UV-B | PpUVR8 expression was not significantly different to the control in both UV-B-treated fruit after exposition, although a slightly higher transcript abundance was detectable 6 h after UV-B exposures | Peach skin        | Santin et al., 2019          |
| Raphanus sativus        | RsUVR8    | UV-B dose was set at 10 W m⁻² | 2x | Hypocotyl | Wu et al., 2016           |
| Solanum lycopersicum    | SlUVR8    | Plants were exposed for 5 min per day to 2.94 kJ m⁻² UV-B (312 nm) during 30 days | 6x | Leaf | Mariz-Ponte et al., 2018 |
| Vitis vinifera          | VvUVR1    | Plants were exposed for 6 h to 15 μW cm⁻² UV-B | No significant changes                                                                 | Leaf              | Loyola et al., 2016          |
| Vitis vinifera          | VvUVR8    | Vines were divided into experimental conditions: no filter (Ambient); UV radiation-transmitting filter (FUV+); UV radiation-blocking filter (FUV-). | No significant changes                                                                 | Fruit skin        | Carbonell-Baejano et al., 2014 |
| Zea mays                | ZmUVR8    | 5-week-old plants were exposed to UV-B (2 W m⁻²) for different periods of time. The first 3 leaves at the top received UV-B radiation while the rest were shielded. | Expression was rapidly increased by UV-B after 10 min in irradiated leaves and shielded leaves. After 4 h of UV-B, expression was down-regulated both in irradiated and shielded leaves. | Leaf              | Casati et al., 2011a,b       |
the transcription of UVR8 and COP1 is dose-dependent, reaching its peak 6 h after UV-B exposure (Contreras et al., 2019).

UVR8 expression is repressed in maize leaves irradiated with UV-B for 1 h (Casati et al., 2011a). However, in the leaves shielded from UV-B, UVR8 expression is induced as part of a systemic response. The induction observed in the shielded leaves is overturned when the plants are exposed to UV-B more than 4 h (Casati et al., 2011a). In eggplant, as in maize, expression of the UVR8 transcript is induced with 0.5 h UV-B exposure and repressed after 4 and 5 h (Li J. et al., 2018).

In radish sprout hypocotyls, the UVR8 expression is induced significantly by UV-B (2 times with respect to the control) (Wu et al., 2016). Expression levels of PpUVR8 did not vary substantially in peach skin during treatment with UV-B, but increased slightly after exposure, reaching the highest peak at 6 h (Santin et al., 2019). In conclusion, there are some species in which UVR8 expression in response to UV-B is constant, as in Arabidopsis, but in most cases the expression levels vary.

**PRESENCE OF RUP1 AND RUP2 IN DIFFERENT SPECIES**

RUP1, RUP2, and COP1 are members of the WD40-repeat protein family. RUP1 and RUP2 contain seven WD40-repeats with apparently no additional domains (Van Nocker and Ludwig, 2003; Li et al., 2013). In the presence of UV-B, levels of RUP proteins increase and their relative abundance (compared to COP1) interrupts the interaction UVR8-COP1, contributing to the reversal of UVR8 from monomer to homodimer. As a result, RUP proteins switch off the signaling cascade, thus averting problems in plant growth and development (Gruber et al., 2010; Heijde et al., 2013). In plants growing in diurnal photoperiods under natural light, a UVR8 dimer/monomer photo-equilibrium is established. In that state, RUP1 and RUP2 play a crucial role in the reversion of monomer to dimer, allowing for the plant's optimum growth and development in that specific environment (Findlay and Jenkins, 2016).

In addition to RUP proteins, STO/BBX24, RCD1, and DHU1 have also been characterized as negative regulators in the Arabidopsis UV-B signaling cascade (Jiang et al., 2009, 2012a,b; Kim et al., 2017). Most studies concerning the characterization of RUP proteins in response to UV-B have been performed in Arabidopsis (Gruber et al., 2010; Heijde et al., 2013; Vanhaevelyn et al., 2016). AtRUP1 (385aa) and AtRUP2 (368aa) proteins have a 64% identity (Favory et al., 2009; Supplementary Table 1) and both fulfill the same functions in the UV-B response (Vanhaevelyn et al., 2016). In order to search for RUP proteins in terrestrial plants, a blastp (blast protein, ncbi) was carried out using AtRUP1 (OAO92149.1) and AtRUP2 (OAO92900.1) as query sequences. As can be observed in Figure 2 and Supplementary Table 1, there are few RUP1 sequences with a high percent identity (91% to 64%). The sequences identified as RUP1 derive from species of the Brassicaceae family, as Arabidopsis. The one exception is a Tarenaya hassleriana sequence, which belongs to a Brassicaceae sister family. The high percent identity values are to be expected since the sequences derive from the same family.

Recently, in experiments with mutants obtained through CRISPR/Cas9, it has been demonstrated that UV-B response in M. polymorpha includes many common components with Arabidopsis, among them RUP1 (Mapoly0094-s0072) (Clayton et al., 2018). In contrast to the RUP1 sequences detected, there is a higher number of RUP2 sequences detected (Figure 2 and Supplementary Table 1). The phylogram shows that RUP1 and RUP2 from monocotyledons and dicotyledons belong to different clusters (Figure 2).

The percent identity in the sequences identified as RUP2 in dicotyledons (93%-53%) is higher than in monocotyledons (lower than 55%). Due to the low percent identity of RUP2 proteins in monocotyledons and the fact that RUP1 sequences have not been detected in this group, it could be hypothesized that RUP proteins would not be part of the switch-off mechanism in monocotyledons.

One hypothesis is that mechanisms such as the ones mediated by STO/BBX24 and DHU1 suffice to switch off the UV-B response. Another possibility is the existence of proteins fulfilling the same functions as RUPs, but with a low percent identity. Yet another proposition is that the negative regulation mechanism could be based on direct repression of UVR8 expression or UVR8 monomer degradation, whenever necessary. Research has demonstrated that, in several species, UVR8 gene expression is regulated in the presence of UV-B (Table 2). In maize, for example, Casati et al. (2011a) reported that, after extended exposure to UV-B, UVR8 expression was repressed both in exposed and shielded leaves, possibly as part of negative feedback.

There are proteins that have a low percent identity but still exhibit conserved domains that allow them to fulfill the same functions. RUP proteins have seven WD40-repeats with apparently no additional domains (Gruber et al., 2010). It was observed that the C27 region of UVR8 interacts with the WD40 region of COP1 and RUP1/2 (Gruber et al., 2010; Cloix et al., 2012). It would be interesting to examine the degree of conservation of the WD40 domain among RUP2 proteins in monocotyledons and dicotyledons, and if it can interact with UVR8 as it does in Arabidopsis.

**UVR8 IN FRUIT DEVELOPMENTAL STAGES**

UV-B is an environmental signal that is perceived by plants, modulating growth, development, and metabolism in different organs (Tilbrook et al., 2013). By studying Arabidopsis mutants, the participation of UVR8 in many of the responses triggered by UV-B in leaf (Wargent et al., 2009), hypocotyl (Li et al., 2019), root (Wan et al., 2018), and flower (Dotto et al., 2018) has been determined, but further research in fruit is required. UV-B promotes flavonoids and anthocyanins accumulation in Arabidopsis and other species (Lois, 1994; Ubi et al., 2006). In Arabidopsis leaves, synthesis of flavonoids and anthocyanins in response to solar UV-B radiation is regulated by the UVR8 receptor (Morales et al., 2013). The production of other pigments, such as carotenoids, is also induced by UV-B (Becatti et al., 2009).
Furthermore, UV-B radiation increases fruit color in several fruit trees like grapes, apples, peaches, and blueberries, among others (Zhao et al., 2016; Escobar et al., 2017; Henry-Kirk et al., 2018). Fruit nutritional quality frequently depends on the content of those pigments, and their composition varies throughout the fruit’s development and ripening (Wang et al., 2008).

In sunlight conditions, anthocyanins accumulate in the pericarp of Litchi chinensis. In Litchi, eight putative UVR8 encoding genes were identified, and their expression increases differentially when the fruit is exposed to UV radiation. The incremental expression of UVR8 is accompanied by the up-regulation of key genes in the anthocyanin biosynthesis pathway. In the skin of apples and eggplants, UVR8 expression increases in response to UV-B, together with a rise in flavonoid and anthocyanin levels. During fruit ripening, UVR8 expression changes (increments and decrements) were reported, suggesting physiological changes do not play a minor role in its regulation (Henry-Kirk et al., 2018; Santin et al., 2019). From this information we can infer that, in the presence of solar UV-B, UVR8 is involved in the skin coloring of litchi, apple and eggplant throughout fruit development.

Li H. et al. (2018) demonstrated that, in response to UV-B, UVR8 in tomato (SIUVR8) induces the expression of genes and the accumulation of light-absorbing compounds in leaves. Tomato plants containing silenced UVR8 (SIUVR8Ri) presented pale-green fruits when grown under natural sunlight. In contrast, in UVR8 over-expressing plants (SIUVR8OE), the fruits exhibited a darker green color compared to the wild-type
(WT). Furthermore, the accumulation of starch, carotenoids, and lycopenes was higher in SlUVR8OE and lower in SIUVR8Ri fruits. The number of chloroplasts per cell was the same in WT and transgenic plants, but plastid size and thylakoid granules increased. The transcriptional factor GOLDEN2-LIKE (GLK2) determines chlorophyll accumulation and chloroplast development in fruits, inducing expression of genes associated to photosynthesis (Waters et al., 2008). When treated with UV-B radiation, SIUVR8 increased both GLK2 accumulation and that of its target genes (Li H. et al., 2018).

Pre and postharvest treatments with UV-B radiation have been employed to induce fruit ripening and pigment accumulation (Castagna et al., 2013). In grape berries, UV-B modifies the quantity and quality of flavonoids, improving their organoleptic properties (Martínez-Lüscherab et al., 2014). UV-B induction of secondary metabolites is not only beneficial to plants but also to human health (Schreiner et al., 2012).

In fruits exposed to UV-B, chloroplasts are larger and starch accumulation is higher, hence influencing the nutritional quality of the fruit in a UVR8 dependent pathway. In addition, it has been observed that, in fruit, UVR8 could induce the synthesis of pigments that absorb UV-B. Since UV-B induces pigment increase and metabolite accumulation, and this impacts directly on production and fruit quality, it would be interesting to examine if these processes are mediated by UVR8.

**DIFFERENT INDUCERS OF UVR8 EXPRESSION**

In Arabidopsis, UVR8 expression increases slightly in response to various abiotic stresses, except for the important increase when osmotic and salt stress are involved (Fasano et al., 2014; Table 3). Expression of the UVR8 transcript and protein levels increase in Arabidopsis plants grown in MS medium with NaCl and polyethylene glycol (PEG) for 24 h. In B. platyphyllo, treatments with ABA and NaCl induced UVR8’s promoter activity, resulting in an increase in BpUVR8 transcript levels (Li X. et al., 2018). Expression of UVR8 gene is induced in foxtail millet cultivar (cv. Prasad) 24 h after salt stress, while in cv. Lepakshi it decreases continuously (Puranik et al., 2011). In leaves of two drought-tolerant barley genotypes (Martin and Hordeum spontaneum 41-1 cultivars), UVR8 transcript levels are higher than in a drought-sensitive genotype (Moroc9-75), but the levels do not change when the three genotypes are exposed to drought stress (Guo et al., 2009). Interestingly, UVR8 expression in barley and millet differ among cultivars of the same species (Guo et al., 2009; Puranik et al., 2011). Under waterlogging conditions, ethylene promotes the formation of lysigenous aerenchyma in the root cortex of Zea mays. ZmUVR8 transcription is induced by waterlogging, mainly in the cortical cells (Rajhi et al., 2011). In radish sprouts, UV-B, cadmium, chilling, and salinity induced the expression of UVR8 (Wu et al., 2016). Additionally, exogenous addition of H$_2$O$_2$ and sodium nitroprusside (SNP, an NO donor) also induced UVR8 expression. This response is inhibited by dimethylthiourea (a H$_2$O$_2$ scavenger) and cPTIO (2-(4-carboxyphenyl)-4,4,5,5-tetramethylimidazoline-1-oxyl-3 oxide, a NO scavenger) (Wu et al., 2016).

In Litchi fruits, differential expression of multiple UVR8 genes has been reported. Although the expression of all these genes is induced by light, maximum transcript levels are achieved at different times (Zhang et al., 2016). White light induces the expression of the UVR8 gene in radish and grape berries, while darkness suppresses it only in grape berries (Azuma et al., 2015; Wu et al., 2016). Loyola et al. (2016), who refer to VvUVR8 as UVRI, showed that UVR8 expression is subject to shading and elevated temperature in Vitis vinifera (grape) berries.

As in Arabidopsis, under shading treatment, the expression of UVR8 does not change significantly in Camellia sinensis tea buds. Interestingly, a unigene annotated as UVR8 LIKE decreases its expression with shading treatment (Liu et al., 2018).

As previously mentioned, UVR8 gene expression changes in response to UV-B radiation and other agents that provoke several stresses (see Tables 2, 3). Based in this information, we suggest that UVR8 acts as the common factor in the cross-talk among multiple stresses.

**UVR8-INDEPENDENT UV-B RESPONSES**

UVR8 is the only UV-B receptor characterized so far (Rizzini et al., 2011), and it has been shown that it mediates a large number of UV-B specific responses (Wargent et al., 2009; Tossi et al., 2014; Li H. et al., 2018). In Arabidopsis leaves exposed to low levels of UV-B, UVR8 regulates the expression of a wide number of key genes in the photomorphogenic and acclimation response. Conversely, under high UV-B doses, the regulation of WRKY, FAD oxide reductase, and UDPgtfp expression is UVR8-independent (Brown and Jenkins, 2008). The expression of these genes varies in response to several abiotic stresses and is induced by H$_2$O$_2$ (Inzé et al., 2011; Chen et al., 2012). ARIADNE 12 (ARI12) belongs to a family of proteins with E3 Ubiquitin ligase activity induced by UV-B (Eisenhaber et al., 2007). In low UV-B fluence rate conditions, ARI12 transcription is induced only in WT and not in the uvr8 mutants, indicating that gene induction is mediated by the UVR8 receptor. On the contrary, with high UV-B fluence rates, ARI12 transcript levels increased in both genotypes. Thus, expression of ARI12 is induced through a UVR8-dependent pathway in low UV-B fluence rate conditions and by an independent one in high fluence rates (Lang-Mladek et al., 2011). Mitogen-activated protein kinase (MAPK) networks are activated by diverse stresses (Holley et al., 2003). Gonzalez Besteiro et al. (2011) demonstrated that UV-B stress activates the signaling cascade mediated by MAPK1 independently from UVR8. When exposed to UV-B doses that cause acute UV-B stress, the MKP1 mutant (mkp1) is hypersensitive to radiation, while the uvr8 mutant is not. On the contrary, at low UV-B doses, the uvr8 mutant is impaired, but the mkp1 mutant is not. This indicates that, in response to damaging UV-B doses, MKP1 has a main role, while UVR8 is more important at low levels of UV-B light. Thus, the mkp1 and uvr8 mutants allow the genetic
### TABLE 3 | Regulatory agents of UVR8 expression in different plants.

| Species          | Gene   | Regulatory agent | Treatment                                                                 | Gene expression (X: fold increase of gene expression compared to control) | Tissue       | References               |
|------------------|--------|------------------|---------------------------------------------------------------------------|---------------------------------------------------------------------------|--------------|--------------------------|
| Arabidopsis thaliana | AtUVR8 | NaCl             | MS medium supplemented with 100 mM NaCl for 24 h.                          | 2.5x                                                                      | Seedling     | Fasano et al., 2014      |
| Arabidopsis thaliana | AtUVR8 | Osmotic stress (PEG) | MS medium supplemented with −0.5 MPa PEG for 24 h.                      | 4.5x                                                                      | Seedling     | Fasano et al., 2014      |
| Arabidopsis thaliana | AtUVR8 | Starvation       | MS in starvation conditions (no sugar/dark) during 24 h                  | 2x                                                                        | Seedling     | Fasano et al., 2014      |
| Betula platyphylla | BpUVR8 | ABA              | 10 μM ABA for 24 h                                                       | at 3 h (3.3x), 6 h (3.6x), 9 h (4.2x), 12 h (3.25x) and 24 h (1.6x)       | 3-week-old seedling | Li X. et al., 2018      |
| Betula platyphylla | BpUVR8 | NaCl             | 100 mM NaCl for 24 h                                                     | at 3 h (8.5x), 6 h (14x), 9 h (10.2x), 12 h (6.1x) and 22 h (12.4x)      | 3-week-old seedling | Li X. et al., 2018      |
| Camellia sinensis | CsUVR8L| Shading          | The nylon black nets with different light transmitting characteristics were placed approximately 1.5 m over the tea plants. The nets were placed when a new round of bud burst started. Tea buds were collected throughout shading treatments. | Significantly decreased at 4 h and 8 h of shading treatment               | Tea buds     | Liu et al., 2018         |
| Litchi chinensis  | LcUVR8 | Light            | Samples were collected from 8-year-old litchi. Uncolored fruits were wrapped in pouches and later unwrapped and exposed to light | Expression level increased after the bags were removed                   | Fruit        | Zhang et al., 2016       |
| Raphanus sativus  | RsUVR8 | Cadmium (Cd)     | Sprouts were subjected to Cd for 12 h in the dark. (Non-specified concentration) | 1.3x                                                                      | Hypocotyl    | Wu et al., 2016          |
| Raphanus sativus  | RsUVR8 | Chilling         | Sprouts were subjected to chilling for 12 h in the dark. (Non-specified temperature) | 1.5x                                                                      | Hypocotyl    | Wu et al., 2016          |
| Raphanus sativus  | RsUVR8 | NaCl             | Sprouts were subjected to NaCl for 12 h in the dark. (Non-specified concentration.) | 1.5x                                                                      | Hypocotyl    | Wu et al., 2016          |
| Raphanus sativus  | RsUVR8 | H₂O₂            | Sprouts were subjected to different concentrations H₂O₂ (0.2 to 10 mM) for 12 h, and then exposed to white light for another 24 h | up-regulated ranging from 0.5 to 10 mM reaching 2.5x at 5 mM             | Hypocotyl    | Wu et al., 2016          |
| Raphanus sativus  | RsUVR8 | NO               | After 36 h dark incubation, the radish sprouts were subjected to 0.5 mM of SNP under white light for 24 h | 3.3x                                                                      | Hypocotyl    | Wu et al., 2016          |
| Setaria italica   | SiUVR8 | Salinity stress  | 21-day-old seedlings were treated with 250 mM NaCl for 1, 3, 6, 10, 24 and 48 h. Two cv. tolerant cv. Prasad and sensitive cv. Lepakshi | cv. Prasad: 5x 24 h after stress. cv. Lepakshi: continuously declined over time | Seedling     | Purank et al., 2011      |
| Solénium lycopersicum | SiUVR8 | UV-A             | Exposure for 4 h per day to 0.8 J/m² UV-A (365 nm) for 30 days           | 2x                                                                        | Leaf         | Mariz-Ponte et al., 2018 |
| Vitis vinifera    | VuUVR1 | Temperature      | Detached grape berries were exposed to 15 and 35°C                       | Expression dramatically down-regulated (more than 3 times)               | Fruit        | Loyola et al., 2016      |
| Vitis vinifera    | VuUVR1 | Dark             | Detached grape berries were exposed to dark                              | Expression down-regulated (3 times)                                       | Fruit        | Loyola et al., 2016      |
| Vitis vinifera    | VuUVR1 | Pathogen infection | Berries infected with Botrytis cinerea and leaves infected with Erysiphe necator or Plasmopara viticola. | Expression down-regulated in berries infected with Botrytis and in leaves infected with Erysiphe. Expression was up-regulated during latent stages of E. necator infection in leaves | Berries and leaves | Loyola et al., 2016      |

(Continued)
dissection of two UV-B response pathways that coordinately determine plant UV-B tolerance.

All this information demonstrates that the participation of UVR8 in the UV-B response is UV-B dose-dependent. UVR8 mediates several responses to low doses of UV-B, while high UV-B doses trigger other adaptive mechanisms. However, other findings suggest there are specific responses to low doses of UV-B that are independent of UVR8. Exposure to UV-B inhibits leaf growth in various plant species (Liu et al., 1995; Searles et al., 2001) due to a reduction in the number of epidermal cells. In both uvr8-2 and WT plants, the number of epidermal cells per leaf is reduced by UV-B, which suggests that the control of epidermal cell division is independent of UVR8 (Wargent et al., 2009). Moreover, by exposing uvr8 mutants to outdoor conditions, it was observed that UV-B radiation affected morphology by a UVR8-independent mechanism (Coffey et al., 2017). At the DNA level, UV-B radiation induces cyclobutane pyrimidine dimer (CPD) formation, which inhibits transcription and replication, and induces mutations. The activity of CPD photolyases is thus essential for protecting genome integrity from UV-B radiation. Expression of the CPD photolyase (PHR) gene is mediated by both UVR8-dependent and UVR8-independent pathways. In uvr8-6 mutants, the expression of AtPHR is induced by low doses of UV-B, which generate CPDS and not ROS (Li et al., 2015).

These responses, which appear at UV-B doses that do not produce oxidative stress and are independent of UVR8, would suggest the existence of new and/or different UV-B receptor/s.

**DISCUSSION**

**UVR8 in Green Algae, Bryophytes and Angiosperms**

The UV-B light receptor has been thoroughly characterized in Arabidopsis since Kliphenstein first identified it in 2002 (Kliebenstein et al., 2002). Over the last 4 years, research on UVR8 has been conducted for other plant species such as apple, tomato, grape, etc. (Loyola et al., 2016; Zhao et al., 2016; Li H. et al., 2018). Employing bioinformatic analyses, the protein’s functional motifs have shown to be widely conserved in green algae, bryophytes, lycophytes and angiosperms (Fernández et al., 2016), but it has not been found in gymnosperms yet. Fernández et al. (2016) suggest that this might be due to the absence of whole genome sequences for gymnosperm species. Gymnosperms are more tolerant than Angiosperms to UV-B injury because their epidermal cells and leaf anatomy are more effective at attenuating UV-B radiation (Bassman et al., 2001). In some outdoor-grown gymnosperms, such as Scots pine and Norway spruce, UV-B radiation has no significant effects on growth or secondary compounds (Turtola et al., 2006). Based on this information, we propose that UVR8 sequences in gymnosperm have not been detected because either the receptor is unnecessary for this group or there is another receptor.

The UVR8 gene copy number changes between plant species. Chlorophytes contain a single copy of UVR8, same as in Arabidopsis, but bryophytes contain two copies. As in bryophytes, 40% of monocot species contain two UVR8 copies and 32% of dicots contain more than one UVR8 copies (Brown et al., 2005; Fernández et al., 2016). The difference in the UVR8 gene copy number among plant species is an interesting subject of debate. There are several articles that show that an increase in gene copy number and polyploidy contribute in the adaptation to stress (te Beest et al., 2011; Soltis et al., 2015; Panchy et al., 2016). Chlorophytes mark the first appearance of the UVR8 gene in the Viridiplantae kingdom (Fernández et al., 2016). Chlorophytes live in water bodies where UV-B is 100% filtered within the first meter of depth (Zellmer, 1995). This group is able to float, thus allowing green algae to regulate the UV-B doses to which they are exposed. The bryophytes were the first terrestrial plants; they were exposed to high UV-B doses and could not avoid the radiation. In this condition, the presence of two UVR8 gene copies could give them an additional UV-B stress tolerance. When higher plants colonized the earth, some of them grew in places characterized by high UV-B doses and others by low UV-B doses. Under this heterogeneous scenario, the loss or gain of a gene copy could be an adaptive advantage. Interestingly, a study of the genome of the marine Angiosperm Zostera marina claims that UVR8 is not present (Olsen et al., 2016). This plant is found in mostly shallow coastal soft bottom environments with reasonably high water clarity to allow growth at a depth enough to filter almost all UV-B light (Short and Coles, 2001).

It will be interesting to evaluate a potential correlation between the number of UVR8 gene copies and the tolerance to

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**TABLE 3 | Continued**

| Species   | Gene     | Regulatory agent | Treatment                                                                 | Gene expression (X: fold increase of gene expression compared to control) | Tissue                      | References               |
|-----------|----------|------------------|---------------------------------------------------------------------------|--------------------------------------------------------------------------|-----------------------------|---------------------------|
| *Vitis vinifera* | VvUVR8 | White light and UV light | Grape berries just beginning to show color were collected and exposed for 10 days to 15°C/Light (15/L). The light was a mix between white light and UV light with continuous irradiation at 80 µmol·m⁻²·s⁻¹ | Light treatment induced the expression of UVR8, whereas dark treatment suppressed this expression | Fruit | Azuma et al., 2015 |
| *Zea mays* | ZmUVR8L | Waterlogging and ethylene | 12 h under waterlogged conditions with or without pretreatment with an ethylene perception inhibitor 1-ethylicyclopropene (1-MCP), or under aerobic conditions. | Waterlogging induced the expression. The expression induced was blocked by 1-MCP treatment. | Root cortical cells | Rajhi et al., 2011 |
UV-B stress or even the diversity of different eco-geographical niches a species can colonize. Elucidating if higher copy numbers of *UVR8* are linked to an increase in the protein levels and if the multiple copies have redundant roles are also important challenges.

At the protein level, *UVR8* has been characterized in Arabidopsis and in other plant species with similar results. However, contrary to Arabidopsis, in *M. polymorpha*, the *UVR8* receptor is mainly present as a monomer in absence of UV-B, probably due to the poor structural stability of the dimer (Soriano et al., 2018). Furthermore, the subcellular localization differs from Arabidopsis, with MpUVR8 found constitutively in the nucleus (Soriano et al., 2018). Despite these differences, both proteins are functional.

Functional motifs that regulate protein stability and localization are conserved between species (Soriano et al., 2018). The observed differences could be attributed to small variations in amino acid sequences localized outside these motifs. This information suggests that amino acid sequences important to *UVR8* behavior could remain unidentified.

**UVR8 Gene Is Differentially Expressed in Plant Organs and Throughout Fruit Development**

*UVR8* expression is ubiquitous in every species analyzed so far (Rizzini et al., 2011; Jenkins, 2017; Table 1). Although in some species *UVR8* expression is constitutive, in other species the expression varies in a tissue- and development-dependent fashion (Table 1). In fruits, for example, *UVR8* expression is induced during development (Table 1). Some plant species have several *UVR8* genes, e.g., litchi fruits (Fernández et al., 2016; Zhang et al., 2016). The *UVR8* gene copy number could account for the differential expression observed in this plant. It will be thus interesting to analyze differences in the relative levels of either *UVR8* transcripts during development.

*UVR8* is expressed and *UVR8* protein is detected in all plant organs (Rizzini et al., 2011). Transcript levels are higher in leaf, flower and fruit than in root (Table 1). This difference between plant organs could be associated with the necessity of the plant to protect itself from UV-B. On the other hand, the detection of *UVR8* transcript in root, an organ that does not receive UV-B light, suggests other functions for *UVR8* beyond light perception. Recently, using a *Nicotiana* silenced roots (irNaUVR8) approach, it has been demonstrated that *UVR8* mediates colonization of *Deinococcus* (Santhanam et al., 2017).

Throughout fruit developmental stages, *UVR8* transcript levels change (Table 1), indicating the possible participation of *UVR8* in this process. Li H. et al. (2018) have determined that *UVR8* improves chloroplast development in the fruit through the regulation of SlGLK2 in tomato grown outdoors. The study of *UVR8* in different species has allowed the identification of new *UVR8* functions demonstrating that *UVR8* not only participates in the perception of UV-B radiation.

**UVR8 Regulates UVR8 Transcript Expression in Different Plant Species**

*UVR8* expression is constitutive in Arabidopsis plants exposed to UV-B (Kaiserl and Jenkins, 2007; Fasano et al., 2014). However, changes in the levels of the *UVR8* transcript were detected in several plants treated with UV-B (Table 2). The levels of *UVR8* transcripts induced by UV-B increase in the first hours of treatment, but later decrease (Table 2). In Zea mays, *UVR8* expression was transient and also systemic in shielded leaves of UV-B exposed plants (Casati et al., 2011a). This information suggests the existence of a mechanism regulating *UVR8* gene expression by UV-B.

*UVR8* transcript level induction is an energetically efficient mechanism in most plants, since the receptor is synthesized only when required. This, however, implies a slower adaptation to UV-B acute irradiation. In Arabidopsis, in turn, constitutive expression and dynamic regulation, which depends on the *UVR8* dimer-monomer equilibrium, allows for an immediate—although more energetically expensive—response (Rizzini et al., 2011). Selection of one strategy in lieu of the other could be due to a difference in tolerance to UV-B and, in some instances, both modes of UV-B acclimation could be active together, depending on the levels of perceived radiation.

RUP1 and RUP2 are negative feedback regulators of the UV-B signaling cascade. Both proteins interact with *UVR8*-COP1, facilitating *UVR8* redimerization (Gruber et al., 2010; Heijde et al., 2013). In monocotyledons, we found RUP2 sequences with percentages of similarity lower than 50% compared to Arabidopsis, but no sequences similar to RUP1 (Figure 2). In this group, *UVR8* activity regulation could be a balance between *UVR8* synthesis and degradation and redimerization mediated by RUPs proteins would not be necessary. Nonetheless, the coexistence of both mechanisms of *UVR8* activity regulation in some plants cannot be ruled out.

**UVR8 Participates in Response to Multiple Stresses**

Several reports have demonstrated that *UVR8* participates in diverse stresses, often in combination with UV-B (Demkura and Ballaré, 2012; Fasano et al., 2014; Santhanam et al., 2017). The metabolites produced in UV-B response mediated by *UVR8* are beneficial when the plant faces other stresses (Demkura and Ballaré, 2012). As shown in Tables 2, 3, *UVR8* expression is induced by UV-B, salinity, starvation, pathogen infection, waterlogging, UV-A, chilling, etc. The regulation of *UVR8* transcript levels in response to different stresses suggests a possible participation of the receptor. The *UVR8* transcript expression in leaves of two barley genotypes tolerant to drought are higher in cultivars *Martin* and *Hordeum spontaneum* 41-1 compared to a genotype sensitive to drought (Moroc9-75) (Guo et al., 2009). The correlation between the *UVR8* expression levels—stress tolerance, and the evaluation of the role of *UVR8* in those stresses have not yet been determined.

ABA plays an important role both in plant development and in response to abiotic stresses (Tuteja, 2007; Trivedi et al., 2016). In plants exposed to high doses of UV-B, ABA production...
is induced, activating NADPH oxidase and generating H$_2$O$_2$, and also increasing NO production, which abates the damage caused by UV-B (Tossi et al., 2009, 2012). In radish hypocotyls, UV-B, H$_2$O$_2$ and nitric oxide (NO) induce UVR8 expression, whereas a chemical trap for H$_2$O$_2$ represses it (Wu et al., 2016). UVR8 transcript expression is induced by salinity, chilling and osmotic stress (Table 3). Interestingly, these stresses are regulated by ABA (Tuteja, 2007). Treatments with ABA, salt stress, high temperatures and UV-B increase the activity of the BpUVR8 promoter in transgenic tobacco leaves (Li X. et al., 2018). ABA could play a key role in the induction of UVR8 expression in abiotic stresses and development. The interaction between ABA and UVR8 should be thoroughly examined. The identification of specific motives in UVR8 promoters of different species could be an approach to identify other regulatory agents of UVR8 transcript expression.

CONCLUSION

The advantage of working with Arabidopsis is evident and, in this particular case, it has facilitated the characterization of UVR8. However, results gathered from different plant species suggest that the results obtained with Arabidopsis cannot be extended wholly to all plants due to the extant diversity. The study of UVR8 physiology in several species beyond Arabidopsis has enabled to establish that:

- UVR8 is highly conserved and is functional in green algae, bryophytes and angiosperms.
- There are species that present more than one copy of UVR8 gene, and in some species the gene can undergo alternative splicing, generating two UVR8 functional proteins.
- The UVR8 gene is expressed differentially in different organs and throughout fruit development.
- UVR8 is involved in several pathways other than UV-B perception. In tomato fruit, for instance, UVR8 regulates the development of the chloroplast and the synthesis of chlorophyll, carotenoids, starch and lycopenes, thus influencing its nutritional quality. In Nicotiana roots, it mediates colonization by Deinococcus.
- UVR8 transcript expression is regulated by UV-B, H$_2$O$_2$, ABA and other stresses.

The information obtained using different plant species show that UVR8 is a versatile molecule involved in perception of UV-B, as well as in developmental and stress processes. However, there is a lack of knowledge regarding UVR8 activity and its importance in these responses. Some important questions that arise are, among others, the following:

- How is UVR8 regulated during these processes?
- Is there a correlation between the UVR8 transcript levels and stress tolerance?
- How does negative feedback work in plant species where RUP 1 has not been detected and RUP2 has a low similarity percentage?
- How does UVR8 participate in developmental processes under natural growth environments?

Only a comprehensive consideration of UVR8 physiology in different species will allow us to bring light into the mechanisms and importance of this key modulator of several aspects involving plant evolution, development and survival. In addition the information derived from the analysis of the conservation and/or the variability of the responses in different plants might be harnessed to improve cultivar management by means of biotechnological approaches.

AUTHOR CONTRIBUTIONS

VT and JR conceived the work and wrote the manuscript, except sections UVR8: from green algae to higher plants and UVR8 in fruit developmental stages. JI wrote section UVR8 in fruit developmental stages UV8-independent UV-B responses. LL contributed in writing the Discussion and reviewing critically the manuscript. HB wrote section UVR8: from green algae to higher plants UVR8: from green algae to higher plants. AE supervised the writing of the manuscript. SP-Á coordinated the work and carried out the native English edition of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpls.2019.00780/full#supplementary-material
Ball, W. T., Alsing, J., Mortlock, D. J., Staehelin, J., Haigh, J. D., Peter, T., et al. (2018). Evidence for a continuous decline in lower stratospheric ozone offsetting ozone layer recovery. *Atmos. Chem. Phys.*, 18, 1379–1394. doi:10.5194/acp-18-1379-2018

Blaère, C. L., Caldwell, M. M., Flint, S. D., Robinson, S. A., and Bornman, J. F. (2011). Effects of solar ultraviolet radiation on terrestrial ecosystems. Patterns, mechanisms, and interactions with climate change. *Photochem. Photobiol. Sci.*, 10, 226–241. doi:10.1039/c0pp0035d

Bassman, J., Robberecht, R., and Edwards, G. (2001). Effects of enhanced UV-B radiation on growth and gas exchange in Populus deltoide Bartr. ex Marsh. *Int. J. Plant Sci.*, 162, 103–110. doi:10.1086/317901

Becatti, E., Petroni, K., Giuntini, D., Castagna, A., Calvezambi, V., Serra, G., et al. (2009). Solar UV-B radiation influences carotenoid accumulation of tomato fruit through both ethylene-dependent and -independent mechanisms. *J. Agric. Food Chem.*, 57, 10979–10989. doi:10.1021/jf090555x

Belkhirad, Y., and Juallais, Y. (2015). The molecular circuitry of brassinosteroid signaling. *N. Plantol.*, 206, 522–540. doi:10.1111/nph.13269

Binkert, M., Kozma-Bognár, L., Terecséki, K., De Veylder, L., Nagy, F., and Ulm, R. (2014). UV-B-responsive association of the Arabidopsis bZIP transcription factor ELONGATED HYPOCOTYL5 with target genes, including its own promoter. *Plant Cell.*, 26, 4200–4213. doi:10.1105/tpc.114.130716

Björn, L. O. (1996). Effects of ozone depletion and increased UV-B on terrestrial ecosystems. *Int. J. Environ. Stud.*, 51, 217–243. doi:10.1080/02713683.1996.9671182

Bo, K., Wang, H., Pan, Y., Behera, T. K., Pandey, S., Wen, C., et al. (2016). SHORT HYPERSENSITIVE TO UV-B (SHP) encodes a SMADH3-like Chromatin Remodeling Factor Regulating Elongation. *Plant Physiol.*, 172, 1273–1292. doi:10.1104/pp.16.00501

Brown, B., and Jenkins, G. (2008). UV-B signaling pathways with different fluence-rate response profiles are distinguished in mature Arabidopsis leaf tissue by requirement for UVR8, HY5, and HYH. *Plant Physiol.*, 146, 576–588. doi:10.1104/pp.107.108456

Brown, B. A., Cloix, C., Jiang, G. H., Kaiserli, E., Heilmann, M., Baxter, K., Brown, B., et al. (2005). A UV-B-specific signaling component orchestrates plant UV protection. *Proc. Natl Acad. Sci. U.S.A.*, 102, 18225–18230. doi:10.1073/pnas.0507187102

Carbonell-Bejerano, P., Diago, M. P., Martínez-Abaigar, J., Martínez-Zapater, J. M., Tardaguila, J., and Núñez-Olivera, E. (2014). Solar ultraviolet radiation is necessary to enhance grapevine fruit ripening transcriptional and phenolic responses. *BMC Plant Biol.*, 14:183. doi:10.1186/1471-2229-14-183

Casati, P., Campi, M., Morrow, D. J., Fernandez, J. F., and Walbot, V. (2011a). Transcriptional, proteomic and metabolomic analysis of UV-B signaling in maize. *BMC Genom.*, 12:321. doi:10.1186/1471-2164-12-321

Casati, P., Morrow, D. J., Fernandez, J., and Walbot, V. (2011b). Rapid maize leaf and immature ear responses to UV-B radiation. *Front. Plant Sci.*, 2:33. doi:10.3389/fpls.2011.00033

Castagna, A., Chiavaro, E., Dall’Asta, C., Rinaldi, M., Galaverna, G., and Casati, P., Morrow, D. J., Fernandes, J., and Walbot, V. (2011b). Rapid maize leaf and immature ear responses to UV-B radiation. *Front. Plant Sci.*, 2:33. doi:10.3389/fpls.2011.00033

Contreras, R. A., Pizarro, M., Kohler, H., Zamora, P., and Zúñiga, G. E. (2019). UV-B shock induces photoprotective flavonoids but not antioxidant activity in Antarctic *Colobanthus quitensis* (Kunth) Bartr. *Environ. Exper. Bot.*, 159, 179–190. doi:10.1016/j.envexpbot.2018.12.022

Demkura, P., and Ballaré, C. (2012). UVR8 mediates UV-B-induced Arabidopsis defense responses against *Botrytis cinerea* by controlling snipate accumulation. *Mol. Plant*, 5, 642–652. doi:10.1093/mp/sss025

Dotto, M., Gómez, M. S., Soto, M. S., and Casati, P. (2018). UV-B radiation delays flowering time through changes in the PRC2 complex activity and miR156 levels in Arabidopsis thaliana. *Plant Cell Environ.*, 41, 1394–1406. doi:10.1111/pce.13166

Eisenhaber, B., Chumak, N., Eisenhaber, F., and Hauser, M. T. (2007). The ring between ring fingers (RBR) protein family. *Genome Biol.*, 8:209. doi:10.1186/gb-2007-8-3-209

Escobar, A., de Oliveira Silva, F., Acevedo, P., Nunes-Nesi, A., Alberdi, M., and Reyes-Diaz, M. (2017). Different levels of UV-B resistance in *Vaccinium corymbosum* cultivars reveal distinct backgrounds of phenylpropanoid metabolites. *Plant Physiol. Biochem.*, 118, 541–550. doi:10.1016/j.plaphy.2017.07.021

Fernández, M. B., Tossi, V., Lamattina, L., and Cassia, R. (2016). A comprehensive phylogeny reveals functional conservation of the UV-B photoreceptor UVR8 from green algae to higher plants. *Front. Plant Sci.*, 7:1698. doi:10.3389/fpls.2016.01698

Findlay, K., and Jenkins, G. (2016). Regulation of UVR8 photoreceptor dimer/monomer photo-equilibrium in Arabidopsis plants grown under photoperiodic conditions. *Plant Cell Environ.*, 39, 1706–1714. doi:10.1111/pce.12724

Frohnmeyer, H., and Staiger, D. (2003). Ultraviolet-B radiation-mediated disruption of cross-dimer salt bridges. *Science*, 335, 1492–1496. doi:10.1126/science.1218091

Gao, W., Zheng, Y. F., Slusser, J. R., and Heisler, G. M. (2003). Impact of enhanced ultraviolet-B irradiance on cotton growth, development, yield, and qualities under field conditions. *Agric. Forest Meteorol.*, 120, 241–248. doi:10.1016/s0168-1923(03)00049

Gonzalez Besteiro, M., Bartels, S., Albert, A., and Ulm, R. (2011). Arabidopsis MAP kinase phosphatase 1 and its target MAP kinases 3 and 6 antagonistically determine UV-B stress tolerance, independent of the UVR8 photoreceptor pathway. *Plant J.*, 68, 727–737. doi:10.1111/j.1365-311X.2011.04725.x

Gruber, H., Heijde, M., Heller, W., Albert, A., Seiditz, H. K., and Ulm, R. (2010). Negative feedback regulation of UV-B-induced photomorphogenesis and stress acclimation in Arabidopsis. *Proc. Natl Acad. Sci. U.S.A.*, 107, 2102–2107. doi:10.1073/pnas.0914353107

Gio, P., Baum, M., Grando, S., Ceccarelli, S., Bai, G., Li, R., et al. (2009). Differentially expressed genes between drought-tolerant and drought-sensitive barley genotypes in response to drought stress during the reproductive stage. *J. Exp. Bot.*, 60, 3531–3544. doi:10.1093/jxb/erp194
leaf development in response to ultraviolet B radiation. *N. Phytol.* 183, 315–326. doi: 10.1111/j.1669-8137.2009.02835.x

Waters, M., Moylan, E., and Langdale, J. (2008). GLK transcription factors regulate chloroplast development in a cell autonomous manner. *Plant Cell* 56, 432–444. doi: 10.1111/j.1365-313X.2008.03616.x

Weber, M., Coldewey-Egbers, M., Fioletov, V. E., Frith, S. M., Wild, J. D., Burrows, J. P., et al. (2018). Total ozone trends from 1979 to 2016 derived from five merged observational datasets – the emergence into ozone recovery. *Atmos. Chem. Phys.* 18, 2097–2117. doi: 10.5194/acp-18-2097-2018

Wu, D., Hu, Q., Yan, Z., Chen, W., Yan, C. Y., Huang, X., et al. (2012). Structural basis of ultraviolet-B perception by UVR8. *Nature* 484, 214–219. doi: 10.1038/nature10931

Wu, G., Bornman, J. F., Bennett, S. J., Clarke, M. W., Fang, Z., and Johnson, S. K. (2017). Individual polyphenolic profiles and antioxidant activity in sorghum grains are influenced by very low and high solar UV radiation and genotype. *J. Cereal Sci.* 77, 17–23. doi: 10.1016/j.jcs.2017.07.014

Wu, Q., Su, N., Zhang, X., Liu, Y., Cui, J., and Liang, Y. (2016). Hydrogen peroxide, nitric oxide and UV RESISTANCE LOCUS8 interact to mediate UV-B-induced anthocyanin biosynthesis in radish sprouts. *Sci. Rep.* 6:29164. doi: 10.1038/srep29164

Yang, Y., Liang, T., Zhang, L., Shao, K., Gu, X., Shang, R., et al. (2018a). UVR8 interacts with WRKY36 to regulate HY5 transcription and hypocotyl elongation in Arabidopsis. *Nat. Plants* 4, 98–107. doi: 10.1038/s41477-017-0099-0

Yang, Y., Yang, X., Jang, Z., Chen, Z., Luo, X., Jin, W., et al. (2018b). UV RESISTANCE LOCUS 8 From *Chrysanthemum morifolium* Ramat (CuUVR8) plays important roles in UV-B signal transduction and UV-B-induced accumulation of flavonoids. *Front. Plant Sci.* 9:955. doi: 10.3389/fpls.2018.00955

Yin, R., Arongaust, A. B., Binkert, M., and Ulm, R. (2015). Two distinct domains of the UVR8 photoreceptor interact with COP1 to initiate UV-B signaling in Arabidopsis. *Plant Cell* 27, 202–213. doi: 10.1105/tpc.114.133868

Yin, R., Skvortsova, M. Y., Loubéry, S., and Ulm, R. (2016). COP1 is required for UV-B–induced nuclear accumulation of the UVR8 photoreceptor. *Proc. Natl. Acad. Sci. U.S.A.* 113, E4415–E4422. doi: 10.1073/pnas.1607074113

Yin, Y., Vafeados, D., Tao, Y., Yoshida, S., Asami, T., and Chory, J. (2005). A new class of transcription factors mediates brassinosteroid-regulated gene expression in Arabidopsis. *Cell* 120, 249–259. doi: 10.1016/j.cell.2004.11.044

Zellmer, I. (1995). “UV-B-tolerance of alpine and arctic Daphnia,” in *Cladocera as Model Organisms in Biology*, eds P. Larsson and L. J. Weider (Dordrecht: Springer), 153–159.

Zhang, H. N., Li, W. C., Wang, H. C., Shi, S. Y., Shu, B., Liu, L. Q., et al. (2016). Transcriptome profiling of light-regulated anthocyanin biosynthesis in the pericarp of itchi. *Front. Plant Sci.* 7:963. doi: 10.3389/fpls.2016.00963

Zhao, C., Mao, K., You, C. X., Zhao, X. Y., Wang, S. H., Li, Y. Y., et al. (2016). Molecular cloning and functional analysis of a UV-B photoreceptor gene, MdUVR8 (UV Resistance Locus 8), from apple. *Plant Sci.* 247, 115–126. doi: 10.1016/j.plantsci.2016.03.006

Zhu, P., and Yang, L. (2015). Ambient UV-B radiation inhibits the growth and physiology of *Brassica napus* L. on the Qinghai-Tibetan plateau. *Field Crop Res.* 171, 79–85. doi: 10.1016/j.fcr.2014.11.006

**Conflict of Interest Statement:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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