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PII: S0168-9452(16)30810-X
DOI: http://dx.doi.org/doi:10.1016/j.plantsci.2016.11.014
Reference: PSL 9526

To appear in: *Plant Science*

Received date: 31-5-2016
Revised date: 28-11-2016
Accepted date: 29-11-2016

Please cite this article as: Dolors Verdaguer, Marcel A.K.Jansen, Laura Llorens, Luis O.Morales, Susanne Neugart, UV-A radiation effects on higher plants: exploring the known unknown, Plant Science http://dx.doi.org/10.1016/j.plantsci.2016.11.014

Review article

UV-A radiation effects on higher plants: exploring the known unknown

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Highlights

- The dependence of plant biomass production under UV-A radiation on genotype and/or further environmental conditions is analysed.
- Protection offered by the leaf structure and/or biochemical composition commonly prevents UV-A induced photosynthetic inhibition.
- UV-A regulates the accumulation of specific phenolic compounds rather than total phenolics.
- The overall lack of correlation between UV-A and UV-B effects does imply distinct molecular and physiological responses under the two wavelength bands.
- The review considers a role of photoreceptors (UVR8, phototropins, phytochromes and cryptochromes) in plant responses to UV-A exposure.

Abstract

Ultraviolet-A radiation (UV-A: 315-400 nm) is a component of solar radiation that exerts a wide range of physiological responses in plants. Currently, field attenuation experiments are the most reliable source of information on the effects of UV-A. Common plant responses to UV-A include both inhibitory and stimulatory effects on biomass accumulation and morphology. UV-A effects on biomass accumulation can differ from those on root: shoot ratio, and distinct responses are described for different leaf tissues. In this paper we analysed inhibitory and enhancing effects of UV-A on photosynthesis, as well as activation of photoprotective responses, including UV-absorbing pigments. UV-A-induced leaf flavonoids are highly compound-specific and species-dependent. Many of the effects on growth and development exerted by UV-A are distinct to those triggered by UV-B and vary considerably in terms of the direction the response takes. Such differences may reflect diverse UV-perception mechanisms with multiple photoreceptors operating in the UV-A range and/or variations in the experimental approaches used. This review highlights a role that various photoreceptors (UVR8, phototropins, phytochromes and cryptochromes) may play in plant responses to UV-A when dose, wavelength and other conditions are taken into account.

Keywords:

Ultraviolet-A; plant biomass; morphology; photosynthesis; photodamage; phenolics

1. Introduction

Solar radiation is a complex mixture of ultraviolet (UV), visible light and infrared wavelengths. Different wavelengths have an impact on plant growth and development in different ways, for example through facilitating photosynthesis, activating specific photoreceptors, and/or causing (mostly damaging) photo-modifications of macromolecules. As a result of the major research efforts focussed on clarifying the impact UV-B (280-315 nm) has on plants, there is now an extensive body of data concerning UV-B mediated cellular damage as well as regulatory responses mediated by the UV-B photoreceptor UV RESISTANT LOCUS8 (UVR8) [1]. However, this knowledge of UV-B responses is not matched by a similar comprehension of UV-A (315–400 nm) responses. In fact, the number of studies targeting plant responses to UV-A are relatively few and, while it may be well known that plants growing in sunlight are exposed to UV-A radiation, the impact of such exposure is mostly unknown, hence the term the "known unknown". This lack of knowledge is disconcerting as, in a natural environment, plants are exposed to 10 to 100 times more UV-A photons than they are to UV-B photons [2]. Moreover, because the UV penetration through leaf tissues increases as wavelength increases, UV-A can reach much deeper target sites in the leaves than UV-B can [3]. Indeed, although UV-A is less efficient than UV-B in mediating some biological responses such as DNA damage, the high UV-A levels reaching the deeper tissues can compensate for the lower reactivity [4]. Conversely, the action spectrum for the UVR8 dependent stimulation of *ELONGATED HYPOCOTYL 5* (*HY5*) transcript accumulation levels drops off sharply at 310 nm in *Arabidopsis thaliana* leaves [5] and there is no real evidence that UV-A can evoke UVR8 mediated responses [5]. Instead, a range of blue-light photoreceptors, such as phototropins and cryptochromes, are readily absorbed in the UV-A part of the spectrum [6] (Fig. 1). However, plant responses to UV-A, mediated by these photoreceptors, have been poorly investigated to date and the literature contains contradictory information. Here, the hypothesis explored was that the responses associated with both UV-B and visible light wavelengths can co-occur once plants have been exposed to the UV-A part of the action spectrum. While it is rather convenient to attribute the variable plant responses to UV-A to the activities of multiple photoreceptors and/or other molecular perception responses, the reality is that experimental approaches are also very diverse, with some studies failing to supply detailed information on the used UV-A spectrum and dose.

Rapid advances in the development of UV-emitting LEDs make it increasingly possible to control the entire light spectrum in which horticultural crops are grown. In theory, this will make it possible for growers to control plant growth and development using UV-A wavelengths. Yet, at present, there is still no comprehensive understanding of the changes to plant physiology and biochemistry that UV-A induces. The main aim of this paper is to examine published work dealing with how UV-A effects plants and to (I) explore the strengths and weaknesses of the approaches used to study the role UV-A plays in modulating growth and metabolism, (II) determine the range of UV-A responses, and (III) determine which further factors (environmental, genetic, etc.) modulate UV-A responses.

2. Physical aspects and experimental approaches

At sea level, 6% of the solar radiation comprises UV. Near the equator the UV-component of sunlight is made up of 95% UV-A and 5% UV-B [2]. The levels of UV-A, as well as those of UV-B, vary with latitude, altitude, solar zenith angle, cloud-cover, season, and time of the day [7]. However, the seasonal variation in UV-A levels is significantly smaller than that of UV-B [2,7]. Also, while the daily solar UV-B flux is restricted to the hours around solar noon, the daily UV-A flux is present during a larger part of the day [2,7]. Consequently, UV-B: UV-A photon ratios display large seasonal and diurnal variations, i.e. higher in the summer and at midday, and lower in the winter and in the early morning or evening [2,7]. Although changes in the UV-A: photosynthetically active radiation (PAR; 400-700 nm) ratio are less pronounced than those in the UV-B: PAR ratio, they are an important consideration in experimental design [8–12].

Basically three types of experimental approaches have been used to study plant responses to UV-A: a) studies performed outdoors where natural UV-exposure is diminished with different kinds of cut-off filters, i.e. field attenuation or exclusion experiments, b) studies carried out outdoors but using supplemental UV lighting, i.e. field enhancement experiments, and c) studies performed in controlled conditions using supplemental PAR and UV lamps (i.e. growth chamber enhancement or greenhouse enhancement experiments). From a spectral perspective, field attenuation experiments are the most relevant as plants receive balanced ratios of UV-A: PAR (and, depending on the treatment, UV-B: UV-A: PAR). Hence, these experiments generate realistic information on

the role UV-A plays in regulating growth and development of individual plants, plant communities or entire ecosystems. Controls without any kind of filter must be included in the design to take into account any possible unwanted side effects from using filters [10,13,14]. Field enhancement experiments can provide information on the biological impacts of high levels of UV-A and/or UV-B radiation. The availability of both UV-A and UV-B emitting lamps makes it possible to separately explore the effects of both types of UV radiation. However, while UV-B lamps have been used in many studies, the use of UV-A emitting lamps in outdoor conditions is less common. Instead, UV-A treatments are mostly controls of UV-B treatments whereby polyester filters block UV-B wavelengths, but transmit the small percentage of UV-A emitted by the UV-B lamps. Using such an approach, the increase in total UV-A relative to solar UV-A is very small, ranging from 0.2 % to 2% on a sunny day [15–18]. Despite the very low extent of UV-A supplementation, several studies have reported significant effects of the supplemental UV-A treatment. It is a matter of discussion whether these low supplemental UV-A doses are responsible for the observed responses. Some claim that factors associated with the filters used i.e. the visible light and/or the thermal radiation emitted by the lamps, could account for these results [19–21]. Yet, there are no studies that have elucidated these factors. Thus, more research is needed to clarify the putative role the small increases in a UV-A dosage might play as an environmental signal that can regulate plant growth (Section 3), morphology (Section 4), photosynthesis (Section 5) and metabolite accumulation (Section 6); especially within the context of the small UV-A variations that transpire with latitude, cloud cover, season and time of day.

When considering temperature, humidity and water supply, growth chamber experiments are the most highly controlled but are the least realistic because plants are typically grown under low PAR and with a wide range of relatively high UV-A doses (see tables S1-S3). A similar problem occurs with greenhouse studies as in this case plants are not exposed to UV-B, hence, the balance between UV-A: UV-B: PAR is greatly modified. Overall, a better awareness of the limitations of each experimental approach is needed when drawing conclusions. More specifically, there is a need for a detailed understanding of the importance the UV-A spectrum used has, especially in studies using supplemental UV-A. Spectral information on the UV-A wavelengths used is commonly lacking, but differs among studies. It cannot be assumed that a photon at 315 nm has the same biological impact as a photon at 400 nm (in fact the erythemal action spectrum shows a decrease of (at least) an order of magnitude difference at the higher wavelength). Thus, the use of different UV-A sources with different emission

spectra, or the use of UV-A attenuation filters with different spectral properties, is likely to result in different results. Similarly, it cannot be simply assumed that a dose-response relationship is linear, and experiments with different UV-A doses may yield distinct results. Moreover, the different measurements performed to characterize UV-A levels (i.e. photon flux, irradiance, different biological weighting functions), represent a major challenge to drawing conclusions when comparing studies. Therefore, published information has to be interpreted with caution. It is necessary to measure action spectra and dose-response curves for UV-A mediated plant responses to (1) successfully fill the present knowledge gap about UV-A radiation effects on plants, and (2) develop weighting functions that will enable standardisation of future exposure studies. However, prior to the photobiological characterisation of UV-A responses, there is a need to identify key molecular and physiological targets of such radiation.

3. Effects UV-A has on plant growth

3.1. Influence of UV-A on biomass accumulation

Plants adjust their metabolism in response to changing environmental conditions, optimising performance under the new conditions, and this may either accelerate or retard biomass production. Few studies have investigated the effects of UV-A on plant biomass production. Analysis of published material (Table S1) reveals a stimulatory effect of UV-A on biomass accumulation (shoots and/or roots) in some species [14,15,22–25], but an inhibitory effect in others [14,20,26–29] (Table S1). Hence, plant growth can respond to UV-A, but available data show that the direction of the response is variable (Fig. 2; Table S1). These variable UV-A responses may be caused by small changes in the balance between multiple, simultaneous UV-A effects, including induced stress [30–32], changes in morphology (section 4), changes in photosynthesis (section 5) and accumulation of phenolic compounds with antioxidative capabilities (section 6). Data analysis revealed no apparent links between the impact of UV-A on plant biomass production, the geographic origin, or the plant life-form, although there is a clear lack of studies on wild growing and/or mature plants (Table S1). Available data do not allow the effect of the UV-A dose to be determined simply because there is insufficient information on the doses of radiation employed, and remediation of this knowledge gap is an important target for future research (Table S1). However, in several cases, distinct effects resulting from UV-A radiation were found when multiple genotypes were compared under similar

radiation conditions (i.e. within one study). Thus, the genotype is clearly a determinant of plant responses to UV-A. This finding was studied in more detail using *A. thaliana* ecotypes [29]. In response to UV-A exposure, biomass accumulation was reduced in four out of the eight ecotypes studied, in some cases by up to 30% and, in three other ecotypes substantial (but not significant) increases in total biomass were observed [29]. In some species, higher biomass accumulation in response to UV-A radiation was related to higher leaf chlorophyll content and photosynthetic activity [22,23] (discussed in section 5 of this paper), which was attributed, in *R. sativus,* to an increase in leaf soluble proteins and an improved soil nitrogen uptake [23]. However, UV-A mediated alterations in biomass accumulation cannot be simply related to photosynthetic activity, as shown in a recent UV exclusion experiment conducted with *Amaranthus tricolor*. Yet, *A. tricolor* is a C_4 species and a high rate of photosynthesis (gas exchange) can reflect mesophyll CO_2 fixation by PEP-Carboxylase, while the observed biomass reduction can be explained by a slight decrease in Rubisco activity observed in the seedlings growing under UV-A [14].

UV-A was found to promote biomass accumulation in the roots of four woody Mediterranean species growing in a glasshouse, but this occurred only when plants were subjected to low levels of irrigation (i.e. mild drought) [25]. A similar observation was made for *Laurus nobilis* [15]. The increase in biomass in *Laurus nobilis* exposed to low UV-A supplementation occurred under mild drought stress, and was attributed to an amelioration in leaf water use efficiency which, in turn, improved the relative water content and/or photosynthetic rates of the leaf. Thus, it is concluded that some UV-A effects on plant biomass are modulated by other environmental factors. Since, as a consequence of climate change, water deficits are predicted to increase in areas such as the Mediterranean Basin, the interactive effects between UV-A and water deficit on plant growth are of particular interest, and these highlight the need for specific multi-factor experiments with realistic variation in the levels of the factors being evaluated.

One clear outcome from the analysis is that UV-B and UV-A mediated effects on biomass production differ (Table S1). Studies in which the effects of both UV-A and UV-B were reported, show that UV-B radiation had either no [15,24] or a negative impact [14,22,24] on biomass accumulation, irrespective of the direction of the UV-A effect. These data reveal that the extensive data-base on UV-B mediated effects on plant biomass production cannot be used to predict the effects of UV-A on biomass. Moreover, the overall lack of correlation

between UV-A and UV-B effects does imply distinct molecular and physiological responses under the two wavelength bands.

In summary, it is clear that UV-A can impact plant biomass accumulation. It is also clear that effects on biomass production depend on further environmental factors, as well as on the species or even on the genotype, as different responses to UV-A are observed within particular studies (e.g. see [29]). Notwithstanding the need for more standardised experimental approaches, the different UV-A responses observed in *A. thaliana* ecotypes, create an opportunity for linking such phenotypic variation to genetic variation via whole genome sequencing [33].

3.2. UV-A initiates changes in resource allocation

UV-A driven changes in biomass accumulation are also linked to changes in resource allocation. Several reports indicate changes in shoot, leaf and stem biomass investment associated with a general reorganisation of vegetative growth mediated by UV-A (Fig. 2). For instance, more biomass accumulated in the branches of UV-A exposed *Glycine max* to the detriment of the main stem [24]. Furthermore, differential partitioning of biomass between shoots and roots in response to UV-A has been reported in various species. For instance, in all four cultivars of *Cucumis sativus* studied [27], UV-A decreased the amount of shoot biomass, although there was no effect on root biomass. Similar results were found in a cultivar of *Triticum sativum* [26] and in four out of the eight *A. thaliana* ecotypes studied [29]. An analysis of the data from the latter study shows that, in different ecotypes, UV-A induced decreases in plant biomass were associated with either increases, decreases or no change in the root: shoot biomass ratio. Thus, the data imply that UV-A effects on root: shoot ratio are distinct from effects on biomass accumulation. It may be argued that predominantly negative UV-A effects on shoot biomass (Table S1) are related to the fact that above ground tissues are directly exposed to sunlight and thus to UV-A. Nevertheless, some studies have actually found that UV-A can promote biomass accumulation in roots, which suggests that UV-A sensitive shoot photoreceptors could be involved in the transmission of long-distance signals to regulate root biomass accumulation. Indeed, the root: shoot biomass ratio doubled in two cultivars of *Glycine max* grown under greenhouse conditions, as UV-A radiation increased root biomass accumulation but inhibited or had no effect on shoot biomass [24]. Similarly, biomass allocated to roots increased by about 17% in *Urtica dioica* growing under

UV-A [34]. Higher biomass investment in roots might improve the competitive effectiveness of individual species for soil resources (Fig. 2). Nevertheless, root biomass decreased without affecting shoot biomass in *Quercus robur* seedlings in a field experiment with UV-A supplementation [20]. Thus, at present there are both reports on increased and decreased root: shoot biomass ratios following UV-A exposure, and any speculation as to the functional significance of such changes must be treated with caution. The fact that different changes in the root: shoot biomass ratio were observed in a single study (i.e. the same experimental set-up and UV-A doses [29]) emphasises the importance of genetic factors in determining UV-A responses (Fig. 2).

4. Morphological responses of plants to UV-A

4.1. Stimulatory effects of UV-A on leaf size

The morphology of shoots and leaves is a key determinant of light capture, and hence photosynthetic productivity. Conversely, light is a major determinant of shoot morphology and this control function is mediated by a range of photoreceptors. Phytochrome mediated effects of red and far-red light on shoot and petiole elongation have been extensively documented [35]. Changes in blue light also control stem morphology, with blue light impeding stem elongation [35]. Additionally, there is a growing body of work on the inhibitory effects UV-B has on stem length, leaf size and leaf anatomy [36]. UV-A also has decisive morphological effects, especially on leaf size and rosette diameter (Fig. 2; Table S1). For example, supplemental UV-A increased rosette diameter substantially (30% -150%) in eight distinct accessions of *A. thaliana* grown indoors under low PAR conditions [37]. Additional supplementation with UV-B led to the more compact UV-B phenotype. Thus, UV-A and UV-B have, respectively, stimulatory and inhibitory effects on *A. thaliana* rosette size, implying distinct underlying mechanisms. Distinct effects of UV-A and UV-B on whole leaf morphology have also been observed in outdoor conditions (Table S1). Using UV wavelength-selective filters, it was found that UV-A increases total leaf area in *Glycine max* [24]. While UV-A mediated increases in plant height and flag leaf area were noted in some *Sorghum bicolor* varieties, decreases were noted in others [38]. Yet, UV-B caused decreases in flag leaf area in all the varieties that were studied. Thus, it appears that stimulatory UV-A effects on leaf size are less consistent than the commonly observed UV-B mediated dwarfing effect. Thus, it can be concluded that UV-A effects on leaf size are distinct from the effects triggered by UV-B; which agrees with what has been reported for plant biomass

production (Fig. 2; Table S1). While UV-B responses have sometimes been considered in the context of increased shading (i.e. decreasing UV-B exposure) [36], effects of UV-A on leaf size seem to achieve the opposite, increased elongation and exposure to light (Fig. 2). Such effects have been attributed to blue/UV-A absorbing cryptochromes that can play a role in shade avoidance [39]. Although there is currently no evidence to support speculation about UV-A playing a functional role in countering the shade-acclimated phenotype, it is nevertheless clear that the UV-B:UV-A ratio is an important factor to take into consideration when designing UV-A experiments.

4.2. Effects of UV-A on leaf morphology and anatomy are genotype dependent

UV-A induced leaf elongation in outdoor grown *A. thaliana* accession Ler-0 comprises both increases in lamina length and width [29]. A non-significant increase in petiole length was also observed. Conversely, decreases in both lamina length, width and petiole length were measured in *A. thaliana* accession Di-1, which displays a UV-A induced decrease in leaf elongation. Thus, UV-A acts in a concerted manner, increasing or decreasing leaf elongation growth in different directions and in different parts of the leaf, suggesting some form of intercellular signalling. However, observing a concerted effect does not necessarily apply to the different tissues that make up the leaf blade. Supplementation studies using axenic, growth-room raised *Phyllanthus tenellus* showed that UV-A exposure enhanced the thickness of the palisade parenchyma and abaxial epidermis but did not affect the thickness of the spongy mesophyll and adaxial epidermis [40]. UV-A, independently of UV-B, stimulated adaxial epidermal thickness and cell length, in the absence of changes in abaxial epidermal anatomy, in six different Mediterranean species grown in a greenhouse where natural solar radiation was supplemented with low levels of UV-A [41]. The data concerning concerted UV-A effects on longitudinal and lateral leaf elongation growth, tissue specific responses and impacts on cell division and expansion, imply that these UV-A responses comprise a coordinated, regulatory response, rather than a local stress effect.

5. Physiological responses of plants to UV-A: effects on photosynthesis

5.1. UV-A as a damaging factor for photosynthesis

The UV-A component of sunlight has traditionally been considered to be damaging for photosynthesis (Fig. 3A), with the photosystem II (PSII) complex being its main target [30–32]. The primary site of direct UV-A damage is thought to be the catalytic Mn cluster of the water-oxidizing complex [30,32], but UV-A also induces the degradation of D1 and D2 protein subunits from the reaction center of PSII (e.g. [42,43]), as well as the damage to Q_A - and Q_B -binding sites [31,44]. Therefore, the harmful effects of UV-A on PSII function result in a decrease in the maximum quantum efficiency of PSII photochemistry, electron transport rate, and also photosynthesis [30]. Decreases in the photosynthetic activity under high UV-A radiation levels might also be caused by a reduction in Rubisco (C_3 species) or PEP carboxylase (C_4 species) content and/or activity and, indirectly, by an increase in the stomatal resistance to the flux of gases, and/or the amount of reactive oxygen species (ROS) (see [45–48] for recent reviews). ROS accumulation can inhibit the *de novo* synthesis of PSII proteins and, thus, the PSII repair process [47]. Because solar radiation contains much more UV-A than UV-B, it has been suggested that UV-A could be the most detrimental component of sunlight for photosynthetic reactions, despite the lower quantum efficiency of UV-A mediated photoinhibitory damage compared to that caused by UV-B exposure [49–51].

5.2. Changing the paradigm: from *in vitro* studies to leaf studies performed in the field

Most studies investigating UV-A mediated inhibition of photosynthetic activities have been performed *in vitro* using isolated chloroplasts or thylakoids (Fig. 3A). Conversely, many studies performed with entire leaves have shown that the protection offered by the leaf structure and/or biochemical composition can partially or totally mitigate photoinhibition caused by UV-A (Fig. 3A). In a study using *Cucurbita pepo*, the rate constant of photoinhibition was ~10 times higher for isolated thylakoids compared to intact leaves exposed to the same UV-A intensity [51]. It was concluded that the UV-screening compounds accumulated in the leaves of field-grown plants were able to eliminate the photoinhibitory effect of solar UV radiation [51] (Table S2). In accordance with this, the photosynthetic response to UV-A treatments (30, 60, 90 and 120 W m^{-2}) decreased over the summer season in *Populus* x *canadensis* saplings, and this was explained by the natural increase in epidermal flavonoids on the adaxial surface of the leaves [52]. In grape leaves (*Vitis vinifera* L.) without UV screening capacity (plants

cultivated in a greenhouse and acclimated to low PAR), natural UV-A and UV-B doses , respectively, inhibited PSII 5-fold and 12-fold more effectively than visible light [53]. However, a week of outdoor acclimation to sunlight resulted in efficient UV screening, with the effectiveness of natural UV-A and UV-B in inhibiting PSII being less than that of visible light.

Photoreceptors, in particular phytochrome, may play an important role in the photoprotection of the photosynthetic apparatus from UV-A [46,54–56]. Indeed, pre-illumination of indoor-grown lettuce seedlings with red light, enhanced the resistance of the photosynthetic apparatus to UV-A [55]. Protection was related to the activation of phytochrome B by red light, which increased the activity of antioxidant enzymes and the leaf content of UV-A-absorbing pigments (mainly flavonoids). Thus, the loss of carotenoids and chlorophylls was diminished in response to UV-A exposure. Similar results have recently been obtained for *A. thaliana* [56]. As with red light, UV-B can also decrease UV-A mediated damage. The UV-B photoreceptor UVR8 contributes to the induction of antioxidant defenses, which in turn may confer UV-A protection [57]. Therefore, it can be concluded that UV-A mediated photodamage to PSII can occur, but that the extent of such damage can be reduced or even nullified by mechanisms that attenuate these wavelengths, such as the accumulation of compounds that absorb UV-A wavelengths [58].

5.3. Stimulatory effects of UV-A radiation on photosynthesis

Under certain environmental conditions, UV-A wavelengths can enhance photosynthetic rates (Table S2) [59–66]. In particular, data analysis suggests that UV-A might have a significant effect on photosynthesis under low (non-saturating) light conditions i.e. in a shady environment, during sunrise, sunset, or under cloudy conditions (Fig. 3B). For instance, UV-A (340 nm) enhanced photosynthetic rates by 8%-10% in *Poa annua*, *Sorghum halepense* and *Nerium oleander* when given simultaneously with a non-saturating background of PAR (500 µmol m^{-2} s^{-1}) [61]. Nevertheless, recent studies showed that, in certain species, the photosynthetic benefits of UV-A can also be observed under high PAR conditions. In *Pimelea ligustrina,* the UV-A content of sunlight increased photosynthetic rates *in situ* by 12% [64]. Solar UV-A also had a positive effect on the leaf photosynthetic rates of some field-grown *Sorghum bicolor* varieties when compared with plants grown under UV exclusion [38]. Accordingly,

photosynthetic carbon assimilation was also increased when branches of mature trees of *Liquidambar styraciflua* and *Acer rubrum* were exposed to supplementary levels of UV-A under field conditions [63].

Earlier studies already demonstrated that epidermal absorption of UV radiation substantially reduced the photosynthetic rate in the UV-A range of the spectrum [60]. In accordance with this, UV-A-induced photosynthesis in *Pimelea ligustrina* occurred as a consequence of the lack of UV-A screening at the leaf surface, which allowed UV-A to directly excite chlorophyll *a* and/or the accessory carotenoid pigment lutein [64]. This was further supported by the results obtained in barley plants with low epidermal UV-shielding [65]. Up to now, three mechanisms have been proposed to explain UV-A-mediated photosynthetic enhancements at low PAR levels (Fig. 3B): 1) direct absorption of UV-A by chlorophylls and carotenoids, which have absorption peaks in the UV-A region [62,67], 2) absorption by photosynthetic pigments of UV-A-induced blue-green fluorescence emitted by phenolic compounds located within the cuticle, or bound in epidermal and vascular tissue cell walls of leaves [61,62,68,69], and 3) increased stomatal opening due to the absorption of UV-induced blue fluorescence by cryptochromes located in stomata [61]. Accordingly, the stimulation of photosynthesis by UV-A would be dependent on the spectral qualities of leaves, especially the transmission of UV-A and/or the penetration of the blue-green fluorescence from UV-A-excited secondary metabolites [64]. It is known that UV-A transmission is influenced by time of the day [70,71], leaf position [72], growth temperature [73], ontogeny [70], species [72–76] and even ecotype [77].

UV-A radiation can also enhance photosynthesis through induced protection of the photosynthetic apparatus under abiotic stress conditions (such as high UV-B levels, drought or strong visible light). Such protection has been related to the UV-A induced activation of the dissipation of excess energy as heat through the xanthophyll cycle, increased levels of UV-absorbing pigments and/or antioxidants, enhanced stomatal conductance and/or the reduction in the functional size of PSII [65,78]. Yet, not all the studies have found that UV-A induces protection against these abiotic stresses [79]. Various factors, including methodological approaches, UV doses, plant species, and the duration of the experiments may explain these contrasting results and consequently this topic clearly deserves further attention in future studies.

6. Biochemical response of plants to UV-A: effects on phenolics

6.1. UV-A regulation of total phenolic content

Plants synthesize and accumulate a diverse range of secondary metabolites, such as phenolic compounds, terpenoids and alkaloids which perform important functions in light acclimation (reviewed by [80]). Data on the UV-A effect on the accumulation of phenolic compounds in annual and perennial species are scarce and incomplete, especially in comparison with the vast amount of existing literature on UV-B induced compounds (Table S3) (among others, [81,82] and references therein). Data analysis revealed that alterations in the total phenolic compounds of the leaf should not be considered a major strategy employed by plants exposed to UV-A, since, in most of the species studied, independently of the experimental set-up and regardless of the plant life-form or its geographic origin, the leaf total phenolic content did not vary in response to UV-A (Table S3). However, different species also appear to regulate their pool of phenolics in distinct ways (Table S3). For instance, while increases in the leaf total phenolic content were described in *Mentha piperita* [83], *Lactuca sativa* [84] or *Ixeris dentate* [85], the opposite effect was observed in a glasshouse experiment conducted with *Pistacia lentiscus* [25]. And yet, no UV-A effect was detected in the five other woody Mediterranean species raised under the same conditions [25]. Moreover, the developmental stage of the leaf also determines the UV-A-regulation of leaf phenolic content as indicated by studies with *Betula pendula* [10] [86]. It should be noted that UV-A doses used in some of the studies analysed here can differ by more than one order of magnitude (Table S3), implying that a UV-A dose effect cannot be disregarded. Even in the absence of a change in the total pool of leaf phenols, structure-specific chemical shifts within this pool were found in *B. pendula* [10] or *Arbutus unedo* [87] exposed to solar UV-A, or in *Laurus nobilis* grown with supplemental UV-A [15]. Thus, changes in individual phenolic compounds, rather than total phenolic content, should be considered to understand the effects of UV-A on plant metabolites.

Studies where the effects of both UV-A and UV-B are reported highlight that both types of UV radiation can cause an increase in the phenolic content [9,84,85]. Similarly, in field attenuation experiments, the exclusion of UV-B resulted in a decrease in phenolic compounds and excluding both UV-B and UV-A magnified that drop in concentration [10,86]. However, the effect of UV-B on the accumulation of phenolics can be distinguished from that caused by UV-A exposure based on induction kinetics. UV-A mediated increases in the total amount of phenolics in *Lactuca sativa* [84] and *Ixeris dentata* [85] are delayed compared to their response to UV-B.

Furthermore, UV-B had a positive effect on the total pool of phenolics in *Sedum album*, whilst UV-A had no effect whatsoever [88]. These results indicate that UV-A and UV-B regulate the total phenolic content of the leaf through different photoreceptors and/or mechanisms (see section 6.3).

6.2. UV-A regulation of flavonoid content

Flavonoids are the main group of phenolics associated with plant responses to UV [89]. They act principally as antioxidants, especially quercetin derivatives and other dihydroxy B-ring substituted flavonoids [90]. Intracellular accumulation of flavonoids at reactive oxygen species production sites (e.g. vacuole, chloroplasts) highlight its important antioxidant function [90,91]. The UV-absorbing properties of flavonoids were previously thought to perform a key role in UV-B protection. Awareness of the very low absorbance of flavonoids in the wavelength band between 280 – 315 nm has now changed this perception [90,92]. Conversely, most flavonoids absorb in the 315 – 400 nm UV-A range [92]. Therefore, it can be argued that UV-A induced flavonoids play a significant role both in UV-A screening and as antioxidants[81,86][81,86][81,86][81,86]. Consistently, UV-A promoted the accumulation of flavonols (the largest class of monomeric flavonoids) in young leaves of *Mesembyranthemum crystallinum* [93], and excluding UV-A decreased total flavonoid concentration and/or specific flavonoids in two betulaceous species [81,86]. Moreover, evidence for a dose-dependent UV-A-regulated accumulation of quercetins or its derivatives has been reported in *Betula pendula* [10] and *A. thaliana* [9]. However, a dose-dependent decrease in extractable flavonoids was also measured in *Brassica napus* leaves following UV-A exposure [94]. Similarly, when compared to plants kept under ambient UV, the leaf content of specific quercetin and kaempferol derivatives in *Laurus nobilis* seedlings decreased under low levels of supplemental UV-A [15]. The reduction in the amount of these flavonoids in *Laurus nobilis* supplemented with UV-A coincided with the activation of other photoprotective mechanisms, such as a reduction in light-harvesting pigments and an increase in the dissipation of excess energy as heat. The latter responses may have lowered reactive oxygen species production and, hence, the requirement for flavonoid compounds with antioxidant activity. Thus, plants may use various mechanisms to regulate flavonoid pools to prevent cell damage induced by UV-A. Moreover, the UV-A-induction of flavonoids appears to be very compound-specific and, as observed for the UV-A effects on leaf total phenolic, regulated in a species-dependent manner (Table S3).

Studies also indicate that other environmental factors (e.g. nutrient and water availability) modulate UV-A effects on flavonoid accumulation. For example, UV-A exposure enhanced flavonoid levels in *Pinus sylvestris* under high, but not low, nutrient availability [95]. Similarly, only under reduced precipitation did solar UVA exposure decrease the leaf content of two quercetin derivatives in the Mediterranean species *Arbutus unedo* [87]. However, further research is needed to understand the role of the complex interactions between UV-A signalling pathways, and those triggered by other environmental factors, and their subsequent impact on the regulation of the flavonoids.

6.3. Photoreceptors and UV-A induced changes in phenolics

The UV-A-mediated changes in phenolic composition are likely to be controlled at multiple levels of gene regulation. At the transcription level, UV-A induces transcript accumulation of those genes involved in the flavonoid pathway including *PHENYLALANINE AMMONIA LYASE* (*PAL*), *CHALCONE SYNTHASE* (*CHS*), *PRODUCTION OF ANTHOCYANIN PIGMENT 1* (*PAP1*), and *DIHYDROFLAVONOL 4-REDUCTASE* (*DFR*) [85,96–100]. Also, post-transcriptionally, the activity of PAL, a key enzyme in the phenylpropanoid pathway, has been increased by UV-A in *Lactuca sativa* [84,85] and *Solanum lycopersicum* [97]. Furthermore, the UV-A-induced accumulation of flavonoids in leaves of *A. thaliana* could be initiated via UV-A absorption through the UV-A/blue light photoreceptor CRYPTOCHROME 1 (CRY1), given that functional CRY1 is required for the expression of *CHS*, the first enzyme committed in the flavonoid pathway [96]. For other UV photoreceptors (e.g. UVR8 and phototropins), there is limited information on how UV-A initiates or interacts with phenolic pathways regulated by these proteins. In line with its role as a UV-B specific photoreceptor, UVR8 is required for the UV-B induction of flavonoids in *A. thaliana* leaves [98,101]. Recent findings also suggest that UVR8 could have an impact on UV-A-mediated changes in phenolics since the *A. thaliana* UV-B photoreceptor mutant *uvr8-2* revealed impaired accumulation of specific quercetin derivatives in plants exposed to solar UV-A [98]. However, additional research is required to mechanistically dissect possible interactions between UVR8 and UV-A signalling pathways controlling metabolite accumulation in plants.

In summary, compared to other wavelengths such as UV-B, blue light, red and far red light, the number of studies measuring UV-A effects on plant metabolites is very limited. Given the distinct effects of UV-B and UV-A

on total and/or specific phenolic content, there is a real need to determine the roles of UV-B and UV-A/blue light photoreceptors and/or signalling pathways in UV-A induced metabolite accumulation through both transcriptome and metabolome analysis. Experiments using wavelength-specific LEDs comprise an up-to-date technology to investigate the response of photoreceptors to different wavelength in the UV-B and UV-A, as well as violet and blue, range. Furthermore, *A. thaliana* photoreceptor mutants can be used to explore mechanisms underlying UV-A responses. Consequently, the principal tools enabling the UV-A mediated accumulation of phenolic compounds and other secondary metabolites are available for researchers.

7. Concluding remarks and gaps in knowledge

Climate change is likely to result in significant variations in the UV-A fluxes that reach terrestrial ecosystems [102–105]. Specifically, it is expected that at low and mid-latitudes UV-A levels will increase mainly due to reduced cloudiness or reduced plant canopy cover [7,106,107]. Hence, a particular challenge will be to identify the effects these changes in UV-A will have on how plant and ecosystems function. Basic knowledge of plant responses to UV-A will be essential as a springboard from which to launch more far-reaching studies into the underlying molecular mechanisms of plant adaptation to light. However, there is currently no consensus concerning plant responses to UV-A. To our knowledge, this is the first review on the effects of UV-A on higher plants and this, in turn, reflects the lack of studies on the subject. Important questions have been raised about some of the experimental approaches used and their suitability to identify plant responses to UV-A. While outdoor exclusion experiments are considered adequate to yield information on UV-A responses, major questions remain concerning outdoor UV-A supplementation experiments in which very low increases of UV-A, due to the use of polyester-wrapped UV-B tubes, are reported. Reservations concerning this type of experiment include the question as to whether the UV-A sensing system has the capacity to detect small increases in UV-A levels against a substantial background of solar UV-A radiation. Responses to very small increases in light *versus* an intense background have been described in studies with vertebrates [108], but it is unknown whether plants possess this capability as well. The possibility that plant UV-A responses in field supplementation experiments might be attributed to the additional UV-A provided on cloudy days should be considered. Under the latter conditions, supplemental UV-A would represent a higher proportion of the light environment experienced by plants. Clearly,

more experiments including different levels of PAR radiation, and so UV-A: PAR ratios, are needed to address this question. Another experimental concern is the lack of rigorous dose-response curves for UV-A effects on plants, the variability of the UV-A spectrum used and how different UV-A wavelengths impact plants. Generating dose-response curves must be a key priority for this field of research in the quest to assess the consequences variations in UV-A levels may have for plants. Accurate action spectra for UV-A responses are mostly lacking, and this hampers both the comparison of individual studies, as well as the establishment of spectral weighting functions. Accurate action spectra and dose-response curves (measured under carefully controlled laboratory conditions) are particularly important, given that both blue and UV-B photoreceptors may be active in this spectral zone. Action spectra can help reveal whether UV-A causes specific responses that are distinct from the effects induced by UV-B and blue radiation which, in turn, may help explain the seemingly contradictory reports on UV-A mediated responses. If nothing else, this review should serve as a stimulus to promote a more rigorous and standardised investigation in this field, to evidence that there is a clear lack of studies and, if possible, to stimulate the scientific community into reaching a consensus on the units and information that should be reported when characterizing the radiation in which plants grow.

Despite questions about the UV-A exposure methods used, some conclusions can be drawn as to the effects UV-A has on plants. UV-A clearly affects both plant biomass accumulation and morphology, although the direction of the responses depends on a plant's genetic background and, possibly, the UV-A dose, and environmental factors such as water availability. UV-A responses are organ specific i.e. in some species, shoots and roots are distinctly affected by UV-A, which might improve water and nutrient absorption and, possibly, interactions with root associated microorganisms. Furthermore, UV mediated induction of UV-absorbing flavonoids results in the photosynthetic process being generally protected from UV-A damage. Indeed, UV-A, just like UV-B, can trigger the accumulation of leaf total phenolics and/or of specific phenolic compounds.

Unlike UV-B, blue light and red light, there is limited information on the specific genetic components associated with UV-A signalling in plants. Future experiments using whole genome expression analysis could help identify the genes involved in UV-A pathways that are different from those used by plants to respond to other wavelengths in the spectrum. Moreover, experiments with photoreceptor mutants may be used to elucidate the contributions of UVR8 and phototropin mediated responses to plant UV-A responses. For example, studies with

an *A. thaliana* UV-B photoreceptor mutant generated the unexpected finding that UVR8 has an impact on UV-A mediated changes in plant metabolites [98].

An important target for future studies would also be to analyse potential interactive effects between UV-A and other climatic factors. This type of information can instigate agricultural practices that attempt to use solar radiation as a tool to acclimate plants to other environmental factors. More studies, especially those in the field in natural conditions, are needed to realistically evaluate the effects of UV-A radiation on plant growth and development, as well as the adaptive relevance of these induced responses.

Acknowledgments

Funding was provided by Spanish Government (CGL2010-2283), University of Girona (MPCUdG2016), the Academy of Finland Center of Excellence in Primary Producers (2014–2019), and Science Foundation Ireland (11/RFP.1/EOB/3303). The authors acknowledge financial support by COST Action FA0906, UV4Growth. The authors also thank Quim Paredes for his help in elaborating the figures.

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Figure legends

Figure 1. Diagram contrasting the spectral regions of erythemally [109] and the new UV plant growth [110] biological spectral weighting (BSW) functions with sensitivity into the UV-A region of the spectrum, and the plant photoreceptors involved in sensing and responding to UV radiation (cryptochromes [111]; phototropins [112]; phytochrome A [113] and UVR8 [1]).

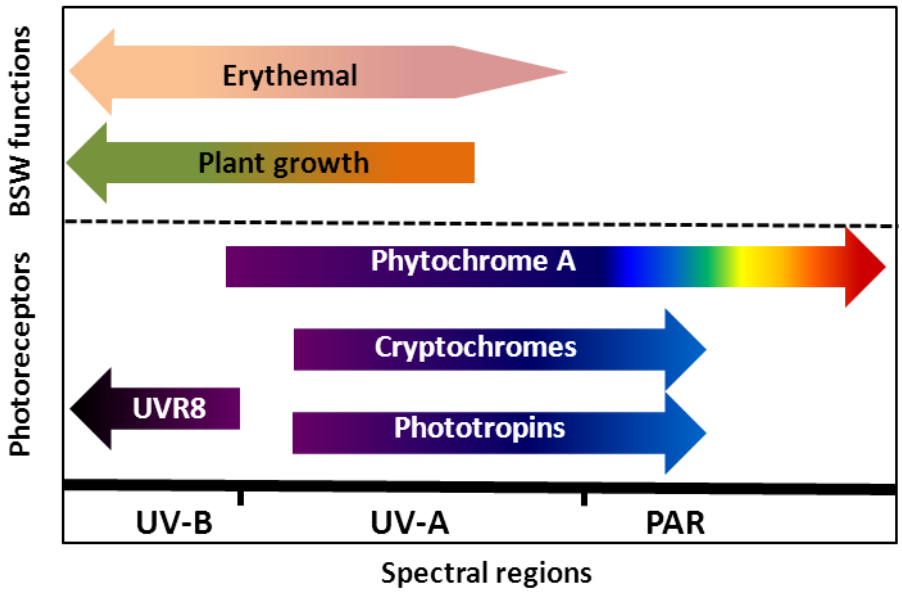

Figure 2. Schematic diagram of UV plant responses on morphology and biomass accumlation. Positive and negative effects on biomass accumulation and morphology are described by UV-A, while UV-B effects are mainly negative. Genetic factors, and possibly also environmental factors, govern changes mediated by UV-A. Changes in plant architecture and biomass allocation can result in changes in resource (light, water and nutrients) uptake.

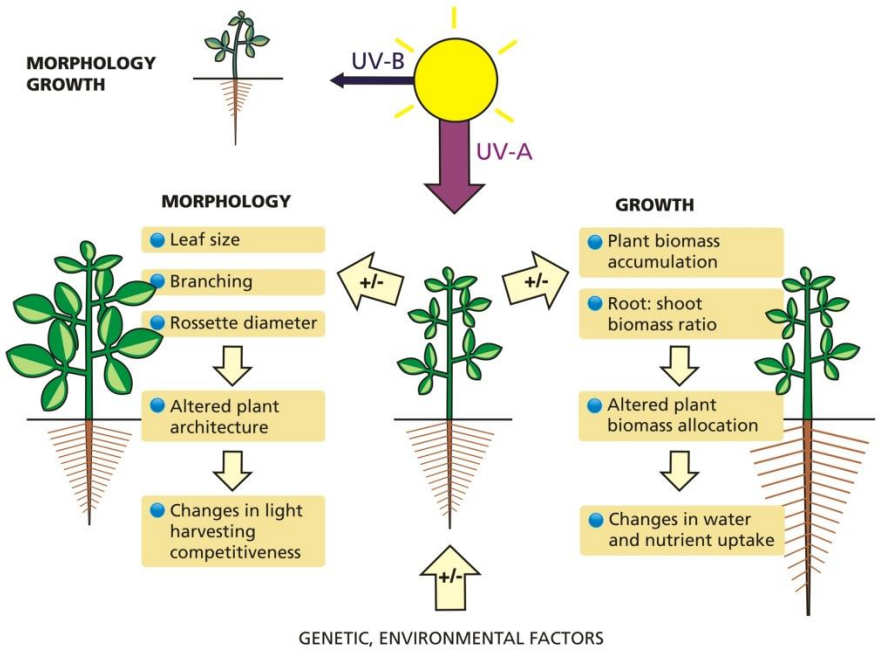

Figure 3. UV-A effects on photosynthesis. A) Under high irradiance, UV-A increases photoinhibition in isolated photosynthetic structures (chloroplasts and tylakoids); conversely, in intact leaves, activation of photoprotective mechanisms (leaf phenolics and antioxidant enzymes) reduces or nullifies photoinhibition. B) Under non-saturing light conditions, (a) direct UV-A absorption by photosynthetic pigments, or (b) absorption by photosynthetic pigments of UV-A induced blue-green fluorescence emitted by phenols, and/or (c) increased stomatal opening could enhance photosynthetic rates.