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Perspective on the influence of ultraviolet radiations in plant growth and development

Introduction

Light is one of the most critical environmental parameters regulating plant growth and development. Photomorphogenesis and photosynthesis are subjected to light intensity, photoperiod, and spectral composition (Paradiso, Proietti, 2021). Compared with light intensity and photoperiod, the impacts of light spectra on modulating plant growth and development are more intricate. Among these different light spectra, blue and red lights are highly absorbed by chlorophyll in leaves, thus driving photosynthesis (Taiz et al., 2014). However, increasing studies proved that, besides blue and red light, other light spectrums such

as ultraviolet (UV) radiation with a wavelength of 200-400 nm critically influence terrestrial plants as well (Verdaguer et al., 2017). In nature, UV radiation comprises three wavebands (UV-A: 315-400 nm, UV-B: 280-315 nm, UV-C: 200-280 nm) (Blaustein, Searle, 2013; CIE, 2020) – Fig. 1.

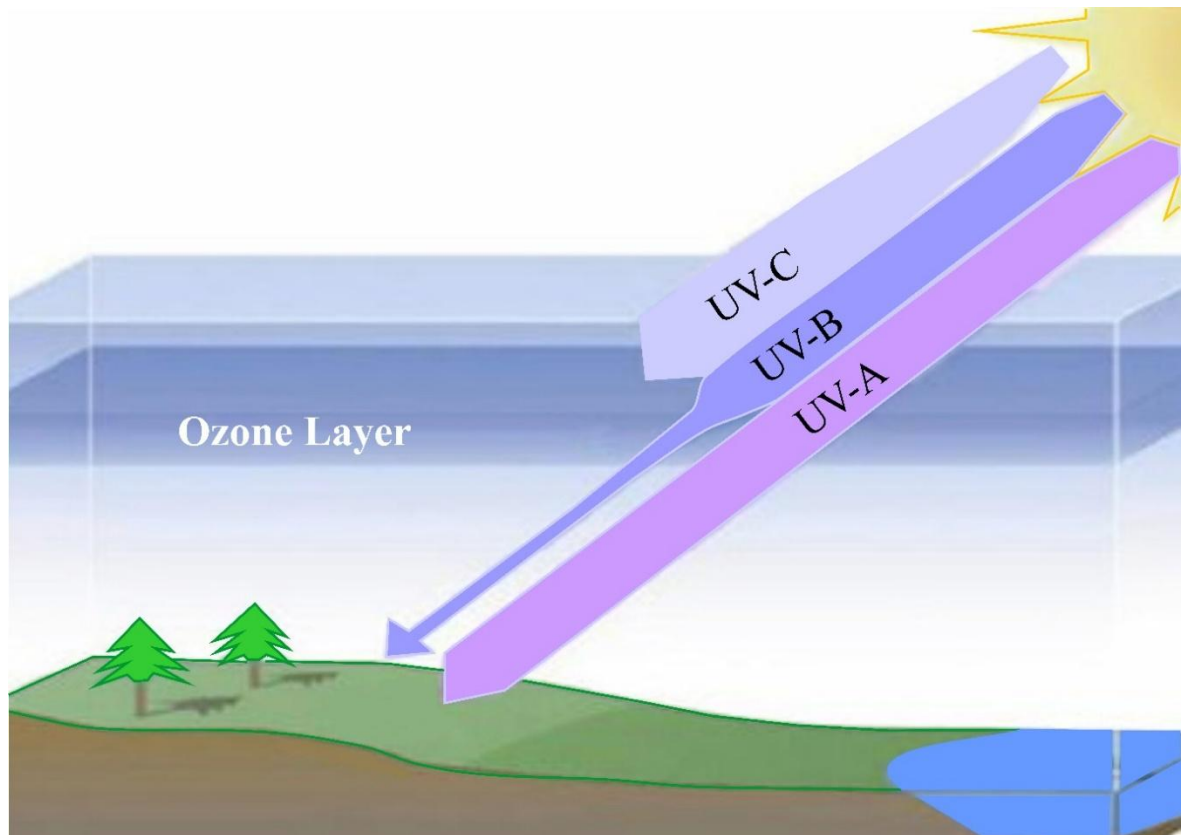


Fig. 1. The penetration of UV-A and UV-B rays to the Earth (Source: www.uvdi.com; modified)

Many studies have centred on plant responses to UV-B and extensive data are now available on the regulatory responses mediated by the UV-B photoreceptor UVR8 (Bernula et al., 2017; Coffey et al., 2017), as well as the retarding impact of UV-B on plant growth (Liu et al., 2011; Huché-Thélier et al., 2016; Vanhaelewyn et al., 2020). Therefore, changes in plant chemistry, such as increased accumulation of flavonoids with high affinity to UV-B and altered epicuticular wax composition, exemplify plants' acclimation responses to UV-B exposure (Gonzalez et al., 1996; Kakani et al., 2003; Bassman, 2004). Despite the widespread distribution of UV-A on the earth and its significant effects on terrestrial plants, consolidated information on plant responses to UV-A is limited (Chen et al., 2019; Rai et al., 2021). Additionally, no definite evidence is available regarding its photoreceptor (Verdaguer et al., 2017), and insofar as the ongoing experiments' results have shown the blue photoreceptors

phototropins and cryptochromes are potential candidates for UV-A absorption (Casal, 2013; Wang et al., 2020).

Plants adjust their physiological and morphological processes in response to altering light conditions, which may suppress or stimulate plant growth (Hogewoning et al., 2010, 2012). Many studies have shown the acceleration of plant growth and modification of plant morphology in response to UV-A radiation (Tezuka et al., 1993; Victório et al., 2011; Chen et al., 2019). For example, plants grown under supplemental UV-A exhibited a larger leaf area index (Antonelli et al., 1997), increased rosette diameter (Biswas, Jansen, 2012; Schulz et al., 2021), and a higher biomass accumulation (Lee et al., 2014; Bernal et al., 2015). The UV-A-induced morphological changes may be attributed to blue/UV-A absorbing cryptochrome, which plays a pivotal role in shade avoidance (Keller et al., 2011). By contrast, some studies reported no significant responses or adverse effects (e.g., prevention of biomass accumulation, leaf expansion, and stem elongation) under the presence of UV-A radiation (Tsormpatsidis et al., 2008; Baroniya et al., 2013); this is likely due to UV-A induced stress (Kreslavski et al., 2013a; Vanhaelewyn et al., 2020). In this context, the direction of plant growth in response to UV-A is not constant. Furthermore, available data do not allow the effect of the UV-A dosage to be determined because of uncertain information on the fluency rates of UV-A radiation involved (Verdaguer et al., 2017). Therefore, it is still unknown whether the growth of plants exhibits a dosage response under UV-A radiation.

Photosynthesis is the ultimate basis for plant growth (Taize et al., 2014). Conventionally, the UV-A component of sunlight has been considered to be detrimental to photosynthesis, as indicated by a decrease in maximum quantum efficiency of PSII photochemistry (F_v/F_m), gas exchange rates, and electron transport rate (Turcsányi, Vass, 2000; Nayak et al., 2003; Kreslavski et al., 2013b). On the other hand, UV-A inclusion generally escalated the photosynthesis rate (Tezuka et al., 1994; Turnbull et al., 2013). Also, under non-saturating (low) light conditions, UV-A can enhance photosynthesis rates (Palma et al., 2021). For instance, UV-A increased the photosynthesis rate by 8-10% in *Poa annua* L., *Sorghum halepense* (L.) Pers., and *Nerium oleander* L. under the background photosynthetic active radiation (PAR) intensity of $500 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Mantha et al., 2001). In this aspect, supplemental UV-A radiation is expected to enhance carbon assimilation in indoor cultivation systems where the background PAR is often far below the light saturation point. Nevertheless,

it is still unknown how UV-A affects the photosynthesis system of individual plants in a controlled environment.

Recently, the rapid development of plant factories with artificial light (PFAL) indicates that various kinds of artificial light procedures are useful during crop cultivation and could affect human development along the feeding pathways (Kato et al., 2010). On the other hand, the vast majority of research on lighting in plant factories has been published with only red and blue radiations (Hernández, Kubota, 2016; reference therein; Trouwborst et al., 2016). Moreover, the ratio of PAR–UV-A, which plays an essential role in the responses of plants to UV-A exposure (Krizek, 2004), is prone to differ to a great extent according to how a plant factory was designed. In retrospect, it remained unknown whether additional UV-A radiation would benefit this indoor cultivation system. As a result, we attempted to provide information on the effect of supplemental UV-A radiation on plant growth and physiology in a controlled environment in this review.

Ultraviolet (UV) radiations

Ultraviolet radiations have been spotlighted because of their vital role in depleting the stratospheric ozone layer, which increases its level on the ground (Rowland, 2006; Bernhard et al., 2010). Consequently, tremendous research efforts have been focused on elucidating the effect of the depleted ozone layer (i.e., increased UV-B level) on plant physiology and agriculture. Primarily, studies were conducted in a chamber, *in vitro*, and in a location that can irradiate high UV-B levels to determine UV-B's damage to plants. Accordingly, it was demonstrated that UV radiations reduce the growth and yield (Teramura, Sullivan, 1994; Caldwell et al., 1998; Kakani et al., 2003a; Gao et al., 2004), destroying cell microstructure (Hollósy, 2002) causing damage, and impairment to photosynthesis processes (Kataria et al., 2014). However, many preceding studies overlooked whether UV-B dosage in nature is harmful enough to underlie the undesirable consequences shown in the chamber studies. As a case in point, it was revealed that the reduction in plant growth by increased UV-B radiation in areas affected by ozone decline, which is the leading cause of an increase in UV level, since 1980 it is unlikely to have gone beyond 6% (Ballaré et al., 2011).

Moreover, an increasing number of researchers are arguing that UV cannot be classified in the category of detrimental plant rays (Jansen, Bornman, 2012), and UV can be

exploited in agricultural lands (Wargent, Jordan, 2013; Thomas, Puthur 2017). Although Montreal Protocol effectively suppressed the emission of ozone-depleting substances and several factors such as cloud and aerosol changes decreased the UV level on the surface these days (Neale et al., 2021), living organisms on the earth are still exposed to higher levels of UV than before. Hence, a need to examine the influence of UV on plants and their coping strategy under UV-induced stresses is required.

Effects of UV on plant growth

Biomass accumulation

Usually, UV-B exposure negatively affects plant growth, developmental processes, and morphology (Zuk-Golaszewska et al., 2003; Cechin et al., 2007; Salama et al., 2011; Chaudhary, Agrawal, 2015; Dotto, Casati, 2017). For example, it was found that the total dry weight of four cucumber cultivars (Krizek et al., 1997), the fresh and dry weight of soybean plants (Zhang et al., 2014; Skórska et al., 2019), and aerial dry mass of lettuce (Tsormpatsidis et al., 2008) were significantly decreased by UV-B in field attenuation studies. An apparent disparity in growth parameters was observed among rice varieties after exposure to UV-B (Hidema, Kumagai, 2006; Faseela, Puthur, 2019). Field enhancement studies have shown that increased UV-B dose can decrease the total dry weight of all wild-type *Arabidopsis* sp. examined (Cooley et al., 2001) and the total biomass of *Coleus forskohlii* Briq (Takshak, Agrawal, 2015), regardless of sampling stages. The same results were observed in soybeans cultivated in a controlled environment with ambient and overall lesser UV-B doses (Biggs et al., 1981). In addition, an examination of the effect of UV dose on the above-ground dry weight of lettuce revealed that as the UV wavelength decreases, the synthesis of biomass is strongly inhibited (Tsormpatsidis et al., 2008). Similarly, longer exposure to some UV-A wavelengths has been linked to an increase in biomass in red-leaf lettuces (Samuoliene et al., 2020).

Contrary to UV-B, which strongly interferes with the accumulation of photosynthates, UV-A tends to be weaker and equivocal; some plants had decreased biomass due to UV-A (Xiong et al., 2001; Kataria, Guruprasad, 2012a), but others remained the same (Zhang et al., 2014) or increased (Kataria et al., 2013; Lee et al., 2014). Although contrasting results limit interpretation, several literature sources confirmed that genetic aspects such as cultivar and

ecotype play a critical role in a plant's sensitivity. In a study where parameters are compared by monocots and dicots or by C₃ and C₄ species, the effects of UV-A were by and large driven by whether a plant is a monocot or dicot, rather than the photosynthetic mechanisms (Kataria et al., 2013). In a study by Häder (1996) who compared the German wheat cultivar and Chilean cultivars grown at high altitudes where UV level is escalated, it turned out that changes in light conditions led to a considerable reduction in the root and leaf dry weights of the German cultivar, implying the presence of a genetic factor that enables UV resistance.

Leaf area/size

There are already abundant reports showing that leaf area, size, or structure is decreased by UV-B (Barnes et al., 1996; Nogues et al., 1998; Cooley et al., 2001; Kakani et al., 2003b; Wargent et al., 2009; Kataria, Guruprasad, 2012b; Klem et al., 2012; Zhang et al., 2012; Fina et al., 2017; Rai, Agrawal, 2017; Rana, Abdulkarim, 2021). With the addition of UV-B rays, reduction in leaf size was mainly associated with the reduced epidermal cell size (Yang, Yao, 2008; Jacque et al., 2011), increased cell wall peroxidase activity, and collateral decrease in the number of cells (Wargent et al., 2009). The effect of UV-B on the leaves of *Arabidopsis* sp. plants was highly attributed to light status after UV treatment (Sztatelman et al., 2015). These authors showed that leaves left in darkness after UV-B treatment had substantially higher chlorophyll content and photosynthetic efficiency than those kept in constant light. Another study, also observed that irradiation of light-emitting diodes substantially increased chlorophyll a and b content, leaf area, and overall growth in lettuce (Miliauskienė et al., 2021). Lately, it was reported that the reduction in leaf expansion in UV-B-irradiated leaves is imputed to the decline in cell production and shortened growth zone (Fina et al., 2017).

Recent studies revealed that UV-A has frequently increased the area and size of leaves (Victório et al., 2011; Zhang et al., 2012; Kataria et al., 2013; Khoshimkhujiev et al., 2014; Zhang et al., 2014), as opposed to UV-B that inhibited leaf expansion. In bean plants, supplemental UV-A stimulated the elongation of leaves and, consequently, resulted in a larger leaf area (Antonelli et al., 1997). This phenomenon is thought to be the upregulation of cryptochrome implicated in shade avoidance, as the absence of blue light led to the reduction in leaf area and the ratio of the lamina to petiole in *Arabidopsis* (Keller et al., 2011). In a study by Brazaitytė et al. (2009), it was identified that UV-A light influenced an enlargement

of leaf area and the amount of secondary metabolites such as phenols, α -tocopherol, and β -carotene in mustard microgreens. Nevertheless, some researchers also reported that the differences in species or genotypes within the same species resulted in various responses such as reduction (Krizek et al., 1997; Qian et al., 2021) and no changes in leaf size (Cooley et al., 2001; Sullivan et al., 2003). Thus, deeper insight into the relationship between cryptochrome and UV-A-induced leaf expansion is needed, which would enable the better exploitation of UV-A by the crop.

Effects of UV on plant physiology

It's not hard to find reports of UV-B radiations resulting in reduced photosynthesis rate (Teramura, Sullivan, 1994; Nogues et al., 1998; Joshi et al., 2007; Kataria, Guruprasad, 2012a; Takshak, Agrawal, 2015; Zhang et al., 2016). Other deleterious effects of UV-B radiation are oxidative stress-induced photosynthetic pigments impairment (Kataria et al., 2014; Kataria, 2017), secondary metabolite variations (Escobar-Bravo et al., 2017), changes in cuticular wax deposition and anatomical characteristics (Nascimento et al., 2015; Willick et al., 2018), extensive harm to photosystem I (PSI) and II (PSII) proteins and disturbance in the electron transport chain (Zhang et al., 2016; Rai et al., 2018). Notably, UV-B has the potential to reduce the maximum quantum yield of PSII ($\Phi_{PSII} \text{ max: } F_v/F_m$), an indicator of the health of the photosynthesis system in higher plants (Keiller et al., 2003; Pfündel, 2003; Lee et al., 2014; Zhang et al., 2016). This is thought as the consequence of photosynthetic components such as photosystem II (Tyystjärvi, 2008; Dobrikova et al., 2013; Kataria et al., 2014) and enzymes involved (Imbrie, Murphy, 1982; Yu et al., 2013; Köhler et al., 2017). Additionally, an appreciable decline in stomatal conductance (g_s) (Nogués et al., 1999; Tossi et al., 2014) and production of reactive oxygen species (ROS) if exposure to UV-B acted as a distress factor in plants (Hideg et al., 2013) were reported as well. The increase in ROS generation in response to UV radiation has been attributed to the disruption of metabolic activities and escalated activity of membrane-localized NADPH-oxidase (Nawkar et al., 2013). Teramura and Sullivan (1994) and Kataria et al. (2014) have provided more detailed information about UV-B-caused deterioration of photosynthesis processes. There are also some indications that augmented CO₂ may alleviate the damaging consequences of UV-B-exposed plants by providing photosynthate and other photoprotective benefits (Qaderi et al., 2005; Koti et al.,

2007; Wargent, Jordan, 2013).

Although some preceding *in vitro* UV-A research indicated that UV-A enhanced photosynthetic activities, there are many opposite cases in that UV-A hindered photosynthesis (Mantha et al., 2001; Joshi et al., 2013; Bernal et al., 2015). The mechanisms underlying increased stimulation of photosynthesis are:

- a) direct absorption of UV-A by chlorophylls and carotenoids (Buschmann, Lichtenthaler, 1998),
- b) indirect absorption of UV-A-induced fluorescence emitted by phenolic compounds (Mantha et al., 2001; Johnson, Day, 2002),
- c) stomatal opening by cryptochromes that perceived the fluorescence (Mantha et al., 2001).

Other alterations corresponding to UV-A-enhanced photosynthesis are increased Rubisco activity in wheat, cotton, and sorghum (Kataria et al., 2013), the higher performance index of photosynthesis (PI_{ABS}) of red lettuce (Lollo Rosso) (Tsormpatsidis et al., 2008), and better yield of electron transport per trapped exciton (ET_0/TR_0) and PI_{ABS} in maize plants (Shine, Guruprasad, 2012).

Interestingly, UV-A was found to have the potential to protect plants from UV-B; When UV-A and UV-B were irradiated together, barley seedlings cultured in weak photosynthetically active radiation exhibited better F_v/F_m and quantum yield of regulated light-induced thermal energy dissipation (Φ_{NPQ}) than ones with UV-B only (Štroch et al., 2015). In cluster bean plants (*Cyamopsis tetragonoloba* (L.) Taub), the ratio of F_v/F_m and oxygen evolution reaction activity that UV-B impaired was restored when UV-A was simultaneously irradiated with UV-B (Gartia et al., 2003; Joshi et al., 2007).

The interaction of other stress factors with UV as a regulator

As the perspective for UV radiation often varies from a stressor to a regulator of plant development, extensive attempts are being made to manipulate UV (Wargent, Jordan, 2013; Kataria et al., 2017; Thomas, Puthur, 2017). One of these attempts, for example, is to ‘vaccinate’ plants with UV radiation to induce cross-resistance to other stress factors (Loconsole, Santamaria, 2021). The interaction between UV and three -representative abiotic stresses – high light, temperature, and water- will be discussed in the following.

High light

Although UV implemented in studies mentioned below appears to have restrained quantitative growth and retarded photosynthetic capacities in plants, UV radiations were proven to be a successful primer to high light stress (Huang et al., 2019). One of the most effective approaches to efficiently use energy by excess light is the xanthophyll cycle (Demmig-Adams, Adams, 1996; Latowski et al., 2011). In barley plants, a bigger pool of xanthophyll cycle pigments and higher flavonoid content diminished the decreases in light-saturated CO₂ assimilation rate (A_{\max} - maximum rate of photosynthesis) and F_v/F_m (Klem et al., 2015). Nevertheless, the xanthophyll cycle barely contributed to the photoprotection in rice upon exposure to high light (Zhao et al., 2017); instead, D1 protein turnover in UV-B-treated leaves was proven as the protective mechanism the plants exhibited due to higher F_v/F_m values (Olsson et al., 2000). In their study on tomato plants, Tao et al. (2021) showed that D1 turnover drives a more critical function than the xanthophyll cycle in photoprotection under sub-high temperature and high light conditions. Apart from the protein turnover, UV-B also increased A_{\max} , which is believed to function as the combination of elevated concentrations of chlorophyll and UV-absorbing compounds (UAC) (Xu, Qiu, 2007). Poulson et al. (2006) found that *Arabidopsis* plants cultivated under UV-B light effectively coped with high light stress; UV-B reduced the loss of photosynthetic capacities expressed by A_{\max} , g_s , F_v/F_m , and transpiration rate (E). Interestingly, this was because UV-B-irradiated seedlings had lower Φ_{PSII} (an indicator of photoinhibition) and higher non-photochemical quenching (NPQ), which lessened non-recoverable photoinhibition (Lal, Edwards, 1996; Niyogi, 1999).

Water

Compared to plants subjected to single stress treatments, the combination of two stresses resulted in less reduction in plant biomass (Bernal et al., 2013, 2015), cuticle thickness (Drilas et al., 1997), needle losses in conifers (Petropoulou et al., 1995), and also helped to sustain photosynthetic apparatuses and needle water relations (Manetas et al., 1997). In several research projects, concurrent UV treatments increased water use efficiency (WUE) and water contents under drought stress. As a case in point, UV-A functioned a critical role in increasing leaf relative water content (RWC) and leaf WUE when *Laurus nobilis* L. plants were subjected to escalated UV-A dose and reduced water supply (Bernal et al., 2015). Plant

photomorphogenic responses to destructive UV-B radiation might be assumed as an adaptative mechanism under conditions akin to high-light environments, such as water stress (Gitz, LIU-Gits, 2003). Not to mention that UV-B's presence under drought helped maintain a better water economy in various species as well (Manetas et al., 1997; Zhao et al., 2009; Bandurska, Cieślak, 2013). This phenomenon was primarily accompanied by thicker leaves (Drilias et al., 1997), lower g_s (Poulson et al., 2002), and increased production of substances such as osmolytes (Schmidt et al., 2000), hormones (Bandurska, Cieślak, 2013), and antioxidant enzymes (Balakumar et al., 1993) which facilitated the adaptation of plants to the extreme environmental conditions.

Temperature

Despite the limited number of research performed, some molecular-based results have been obtained revealing that UV-B robustly weakens thermomorphogenesis (i.e., stem elongation), which shows symptoms similar to shade avoidance signaling, elicited by high temperature (Favory et al., 2009; Hayes et al., 2017; Tavridou et al., 2020). Apart from these molecular proofs, some reports prove amelioration in temperature damage in seedlings receiving UV-B. For instance, young conifer seedlings grown under additional UV-B were more tolerant both to chilling and heating stresses and maintained higher F_v/F_m values compared to those exposed to ambient level UV-B (L'Hirondelle, Binder, 2005). A similar increase in F_v/F_m was also observed in lettuce seedlings in an experiment simulating the heat and high PAR radiation stressors caused by nursery-to-greenhouse transfer (Wargent et al., 2011). Moreover, seedlings pre-acclimatized to UV-B inclusive environment showed relatively higher photosynthetic and growth rates than those pre-acclimatized to UV-B depleted environments (Wargent et al., 2011; Müller et al., 2013). When cucumber seedlings were cultivated in a growth chamber supplemented with UV-B radiation, more seedlings survived heat stress and were taller than those that did not receive UV-B. Such a phenomenon was followed by no alterations in the level of malonaldehyde (MDA) and by a lower membrane injury index in cucumber plants under UV-B exposure (Teklemariam, Blake, 2003). In a study by Neugart et al. (2014), it was found that the combined effect of moderate UV-B ($0.75 \text{ kJ m}^{-2} \text{ d}^{-1}$) and temperature (15°C) substantially increased the mRNA expression of flavonol 3'-hydroxylase in Kale (*Brassica oleracea* var. *sabellica*). Lastly, in soybean plants grown under high

temperatures, electrolyte leakage, expressed as relative injury to tissue in this research, was also alleviated by additional UV-B radiation (Koti et al., 2007). Furthermore, this UV-B supplementation reduced the net CO₂ assimilation (A_n) by heat stress.

Conclusion

As a crucial constituent of light, ultraviolet radiation (UV) has a significant impact on plant general growth and development in many different ways. UV-B, a component of UV light, has been strongly linked to plant growth interference through decreasing biomass accumulation, photosynthesis impairment, and plant physiology disruption (Tab. 1). On the other hand, another light component (UV-A – Tab. 2) has been shown to upregulate the plant's photosynthetic process, increase its resistance to several environmental stresses and have the potential of protecting the plant against the harmful effect of UV-B when illuminated together. Furthermore, it can be concluded that cross-talking these two important light components can enhance water efficiency and alleviate problems linked to thermal stress. Thus, utilizing the importance of ultraviolet radiations, particularly UV-A and UV-B, could assist in promoting plant growth and development, particularly in an enclosed environment.

Conflict of interest

The authors declare no conflict of interest related to this article.

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Perspektywy wpływu promieniowania ultrafioletowego na wzrost i rozwój roślin

Streszczenie

Coraz więcej dowodów wskazuje na wielowymiarową rolę promieniowania ultrafioletowego we wzroście i rozwoju roślin. Ultrafiolet-A (UV-A) jako główny składnik promieniowania UV w przyrodzie, ma szeroki zakres wpływu na rośliny. Ponieważ istnieją pewne dowody wskazujące na jego pozytywne działanie jako regulatora rozwoju roślin w kontrolowanym środowisku, od dawna obserwuje się zainteresowanie wykorzystaniem UV-A w rolnictwie. Jednak rola UV-A we wzroście roślin pozostaje w dużej mierze nieznana, a liczba badań zajmujących się wpływem UV-A w kontrolowanym środowisku jest nadal zbyt mała. Przeprowadzony tu

przegląd ilustruje również wpływ innych składników UV na wzrost, morfologię i fizjologię roślin, takich jak: UV-B, a także wzajemne oddziaływanie innych stresów abiotycznych i UV-A, jako regulatorów wzrostu. Na podstawie przedstawionej tu syntezy można stwierdzić m.in., że niższe dawki promieniowania UV-A mogą stymulować wzrost roślin w kontrolowanym środowisku. Być może przyczyni się to już wkrótce do optymalizacji receptury uprawy roślin w pomieszczeniach.

Słowa kluczowe: akumulacja biomasy, fizjologia roślin, czynniki stresowe, promieniowanie słoneczne

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Abbreviations

Amax – maximum rate of photosynthesis; E – transportation rate; UV – ultraviolet radiations; PS – Photosystem, PAR – photosynthetic active radiation; ROS – Reactive oxygen species, NADPH – Nicotinamide adenine dinucleotide phosphate; UAC – UV-absorbing compounds, WUE – Water use efficiency, RWC – Relative water content, MDA – Malonaldehyde, mRNA – Messenger ribonucleic acid.

Appendix 1

Tab. 1. Comparison of the neutral, positive and negative effects of ultraviolet light (UV-A: 315–400 nm) on plant development; the table presents sample studies

No. Succ.	Plant parameters	The way of impact		
		Neutral	Positive	Negative
1.	Leaf area indicators	Cooley et al., 2001; Sullivan et al., 2003; Tsormpatsidis et al., 2008; Baroniya et al., 2013	Antonelli et al., 1997; Victório et al., 2011; Zhang et al., 2012; Kataria et al., 2013; Khoshimkhujiev et al., 2014; Zhang et al., 2014	Krizek et al., 1997; Qian et al., 2021
2.	Leaves rosette diameter		Biswas, Jansen, 2012, Schulz et al., 2021	
3.	Biomass	Tsormpatsidis et al., 2008, Baroniya et al., 2013; Zhang et al., 2014	Kataria et al., 2013; Lee et al., 2014; Bernal et al., 2015	Xiong et al., 2001; Kataria, Guruprasad, 2012a
4.	Stem elongation	Tsormpatsidis et al., 2008; Baroniya et al., 2013		
5.	Photosynthesis efficiency		Tezuka et al., 1994; Buschmann, Lichtenthaler, 1998; Mantha et al., 2001; Johnson, Day, 2002; Kataria et al., 2013; Turnbull et al., 2013; Palma et al., 2021	Turcsányi, Vass, 2000; Mantha et al., 2001; Nayak et al., 2003; Joshi et al., 2013; Kreslavski et al., 2013b; Bernal et al., 2015
a.	Maximum PSII Quantum Efficiency (Fv/Fm)		Gartia et al., 2003; Joshi et al., 2007; Štroch et al., 2015	
b.	Gas exchange rate		Nayak et al., 2003	
c.	Electron transport rate		Shine, Guruprasad, 2012	
6.	Water Use Efficiency (WUE)		Bernal et al., 2015	
7.	Relative leaf water content (RWC)		Bernal et al., 2015	

Tab. 2. Comparison of the positive and negative effects of ultraviolet light (UV-B: 280–315 nm) on plant development; the table presents sample studies

No. Succ.	Plant parameters	Positive under water or temperature stress	Negative
1.	Leaf area indicators		Barnes et al., 1996, Nogues et al., 1998, Cooley et al., 2001, Kakani et al., 2003b, Yang, Yao, 2008, Wargent et al., 2009, Jacque et al., 2011, Kataria, Guruprasad, 2012b, Klem et al., 2012, Zhang et al., 2012, Fina et al., 2017, Rai, Agrawal, 2017, Rana, Abdulkarim, 2021
2.	Stem elongation		Favory et al., 2009, Hayes et al., 2017, Tavridou et al., 2020
3.	Biomass		Biggs et al., 1981, Krizek et al., 1997, Cooley et al., 2001, Hidema, Kumagai, 2006, Tsormpatsidis et al., 2008, Zhang et al., 2014, Takshak, Agrawal, 2015, Faseela, Puthur, 2019, Skórska et al., 2019,
4.	Photosynthesis efficiency	Wargent et al., 2011; Müller et al., 2013, Sztatelman et al., 2015;	Teramura, Sullivan, 1994, Nogues et al., 1998, Joshi et al., 2007, Kataria, Guruprasad, 2012a, Kataria et al., 2014, Takshak, Agrawal, 2015, Zhang et al., 2016
a.	Chlorophyll content	Sztatelman et al., 2015	Kataria et al., 2014, Kataria, 2017
b.	Maximum PSII Quantum Efficiency (Fv/Fm)	L'Hirondelle, Binder, 2005; Wargent et al., 2011; Müller et al., 2013	Keiller et al., 2003, Pfündel, 2003, Tyystjärvi, 2008, Dobrikova et al., 2013, Lee et al., 2014 Kataria et al., 2014, Zhang et al., 2016, Rai et al., 2018
c.	Electron transport rate		Zhang et al., 2016, Rai et al., 2018
5.	Stomatal conductance		Nogués et al., 1999, Tossi et al., 2014
6.	Water management	Manetas et al., 1997; Zhao et al., 2009; Bandurska, Cieślak, 2013	