The Role of UV-B Radiation in Modulating Secondary Metabolite Biosynthesis and Regulatory Mechanisms in Medicinal Plants

Guangli Wang,[a] Xiaodan Sun,[b] Yang Li,[c] Yuling Wang,[a] and Changhao Jin [a,]*

The impact of UV-B (Ultraviolet-B) radiation is reviewed relative to the biosynthesis and regulation of secondary metabolites (SMs) in medicinal plants. Plants sense UV-B radiation through the photoreceptor UVR8, which is present as a dimer in the absence of UV-B and monomerizes upon UV-B exposure, interacting with proteins to regulate gene expression. In medicinal plants, UVR8-mediated signaling can regulate the activity of key enzymes, thereby affecting accumulation of secondary metabolites. For instance, in *Arabidopsis thaliana*, UVR8-mediated signaling regulates the expression of flavonoid biosynthesis genes. UV-B radiation influences the yield of SMs in medicinal plants, impacting the biosynthesis of phenolics, terpenoids, and alkaloids, though the effects vary under different UV-B conditions. Furthermore, UV-B radiation induces gene regulation in secondary metabolism, with most genes being upregulated. UV-B interacts with other stress factors, *e.g.* chromium, UV-A, water availability, and temperature, which affect the accumulation of secondary metabolites. However, these mechanisms are complex and require further investigation. Current research exhibits limitations, including uneven study coverage, a lack of standardized methodologies, and insufficient exploration of interactions between UV-B and other factors. Future studies should expand the research scope, adopt multifactorial approaches, and investigate molecular mechanisms, thereby advancing agricultural practices and the development of medicinal plants.

DOI: 10.15376/biores.20.2.Wang

Keywords: UV-B; UVR8; Medicinal plants; Secondary metabolites; Regulatory mechanisms

Contact information: a: Yanbian University, Yanbian 133000, China; b: Jilin Provincial Cancer Hospital, Changchun 130012; c: Agricultural College of Yanbian University, Yanbian 133000, China;
** Corresponding author: 1994188590@qq.com*

INTRODUCTION

Ultraviolet (UV) radiation, as a specific wavelength range of electromagnetic radiation, possesses unique energy properties. In particular, the UV-B band delivers photon energy capable of precisely interacting with electrons in chemical bonds. This interaction induces electronic excitation, where bonding electrons transition to anti-bonding orbitals, thereby reducing the stability of chemical bonds and significantly enhancing chemical reactivity. Consequently, compounds become more susceptible to reactions such as degradation and isomerization. In plant systems, these molecular-level changes triggered by UV-B radiation act as a “key” that unlocks a suite of complex stress and adaptation mechanisms, particularly within the realm of secondary metabolism. The following sections will delve deeply into the critical regulatory mechanisms underlying these processes in medicinal plants, aiming to bridge knowledge gaps and advance research on medicinal plants towards precision and scientific innovation.

Medicinal plants, as the cornerstone of traditional medicine, have been cherished for centuries and remain indispensable resources in modern healthcare and agriculture. Their importance lies in their abundant secondary metabolites, which play essential roles in plant growth, development, and reproduction. These metabolites also exhibit diverse ecological functions, such as defense against herbivores and pathogens, while their therapeutic properties have long been valued by humans (Munasira Begum *et al.* 2022). Secondary metabolites primarily include terpenoids, alkaloids, and phenolic compounds, each characterized by unique chemical structures and distinct medicinal properties. Remarkably, over 25% of modern drugs are derived from plant secondary metabolites, and the pharmacological effects of medicinal plants largely depend on these compounds (Yeshi *et al.* 2022). Hence, investigating the biosynthetic mechanisms of secondary metabolites is vital for medical applications (Wink 2015; Zhaogao *et al.* 2023). However, the synthesis of secondary metabolites is significantly influenced by biotic and abiotic factors, with plants producing these compounds to cope with environmental stresses such as UV radiation, salinity, light, and temperature fluctuations (Thakur *et al.* 2019). This adaptive response not only underpins plant survival but also creates opportunities for the discovery and development of novel pharmaceuticals, serving as a crucial bridge between traditional and modern approaches to health (Yeshi *et al.* 2022).

Among various abiotic stressors, UV-B radiation is one of the most important environmental factors influencing the secondary metabolism of plants. Exposure to elevated levels of solar UV-B radiation induces significant physiological, biochemical, and molecular changes in plants (Wong *et al.* 2019). Consequently, understanding the adaptive mechanisms of plants to UV-B radiation has become particularly critical in the context of global climate change (Liaqat *et al.* 2024). At the molecular level, plant responses to UV-B involve multilayered regulation, encompassing photomorphogenesis, leaf development, cell expansion, and the biosynthesis of secondary metabolites. For instance, UV-B radiation enhances the concentrations of UV-absorbing compounds and anthocyanins in plant tissues, which play key roles in mitigating UV damage (Song *et al.* 2023). Additionally, UV-B modulates antioxidant enzyme activities and induces DNA repair mechanisms, thereby strengthening plant stress tolerance. Studies utilizing model plants and mutants to explore UV-B signaling pathways provide a molecular foundation for comprehensively understanding plant UV-B responses and facilitate the application of these findings in sustainable agriculture (Wargent and Paul 2007).

In summary, UV-B-driven changes in secondary metabolism in medicinal plants hold significant research value. This review aims to summarize the effects of UV-B radiation, both at varying intensities and through supplementation, on the biosynthesis and accumulation of secondary metabolites in medicinal plants, while evaluating its role in inducing secondary metabolism. Furthermore, the review discusses the core regulatory mechanisms of secondary metabolism under UV-B radiation, including UV-B perception, signal transduction, photomorphogenesis, and the activation of transcription factors, with the goal of providing a reference framework for further investigation into the regulatory networks of UV-B.

How Plants Perceive UV-B

UV-B radiation, ranging from 280 to 320 nm in the solar spectrum, significantly impacts plant growth, secondary metabolism, and adaptability to stress. Plants perceive UV-B radiation through the photoreceptor UVR8, which initiates corresponding signaling and transduction processes in response to environmental changes (Rizzini *et al.* 2011) .

Most studies on *Arabidopsis thaliana* indicate that UVR8 is a 440-residue protein characterized by a seven-bladed β-propeller core, a flexible C-terminal region consisting of 60 residues, and a short N-terminal extension (Gong and Zheng 2021).

Regulatory Mechanism of UVR8 Signaling

First, the fundamental molecular mechanisms of the UV-B signaling pathway are elucidated. UV-B Perception As a photoreceptor, UVR8 is capable of sensing UV-B radiation. In the absence of UV-B, UVR8 exists in a dimeric form; however, UV-B irradiation triggers the monomerization of UVR8 (Podolec *et al.* 2021; Zhang *et al.* 2023). Activation of UVR8 following UV-B exposure, UVR8 monomerizes and undergoes a conformational change, enabling interaction with proteins such as COP1 and initiating signaling pathways (Podolec *et al.* 2021; Zhang *et al.* 2023).

Interaction with COP1

The binding of UVR8 to COP1 represents a critical step in UV-B signal transduction. COP1, an E3 ubiquitin ligase, suppresses photomorphogenesis in the dark; however, under UV-B irradiation, the interaction with UVR8 alters COP1's function, thereby affecting downstream signaling (Lin *et al.* 2020; Zhang *et al.* 2023).

Signal transduction

The activation of UVR8 leads to interactions with various proteins, including transcription factors and signaling molecules. These interactions result in the activation or suppression of transcription factors, subsequently regulating the expression of UV-B-responsive genes (Yang *et al.* 2019; Fang *et al.* 2022; Zhang *et al.* 2023).

Gene expression regulation

The ultimate outcome of UV-B signaling is the regulation of a series of gene expressions involved in plant growth, development, secondary metabolism, and stress responses. For instance, COP1 can independently suppress plant photomorphogenesis by promoting the degradation of the transcription factor HY5 (Jenkins 2014). However, under UV-B radiation, when COP1 interacts with UVR8 monomers, HY5 is no longer subjected to COP1-mediated degradation (Pandey *et al.* 2023b). In the regulation of plant secondary metabolism, UV-B can promote the accumulation of flavonoids and anthocyanins, thereby enhancing the plant's ability to withstand UV radiation (Yang *et al.* 2019).

Multiple roles of COP1

In addition to its involvement in UVR8 signaling, COP1 may influence the UV-B signaling pathway through additional mechanisms. Research indicates that certain domains of COP1 are crucial for the nuclear localization and signaling of UVR8 (Zhang *et al.* 2023).

Role of RUP proteins

RUP proteins competitively bind UVR8 with COP1, affecting the nuclear retention and signaling of UVR8. The expression of RUP proteins is induced by UV-B and may play a role in the negative feedback regulation of UVR8 signaling (Lin *et al.* 2020; Fang *et al.* 2022).

C-terminal domain of UVR8

The 17 amino acids at the C-terminal (C17) of UVR8 can interfere with the interaction between the active region C27 of UVR8 and COP1, thereby inhibiting UV-B signal transduction (Lin *et al.* 2020).

Dynamic nuclear localization of UVR8

Under UV-B exposure, UVR8 is rapidly transported from the cytoplasm to the nucleus and accumulates within the nucleus. This dynamic change is crucial for the physiological and metabolic functions of UVR8 (Podolec *et al.* 2021; Fang *et al.* 2022).

UVR8 Signaling Regulates Secondary Metabolism in Medicinal Plants

Building on the elucidation of the UV-B signaling pathway, its role in the secondary metabolomics of medicinal plants is explored, with UVR8-mediated signal transduction playing a particularly critical role.

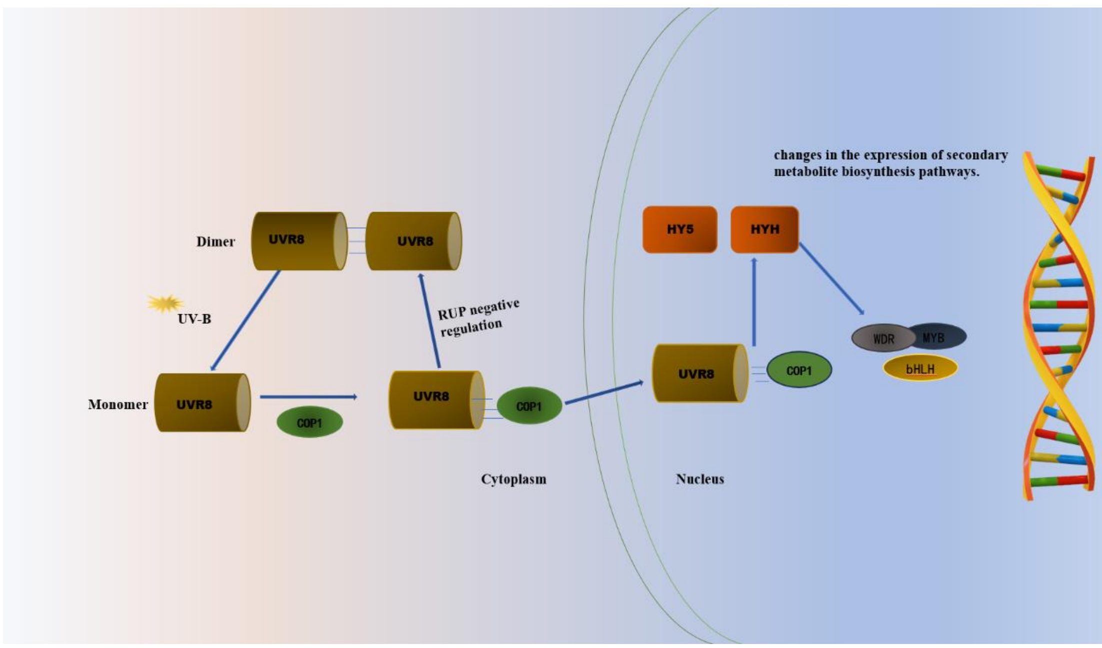

Fig. 1. UVR8-mediated signaling pathway for plant secondary metabolite biosynthesis (Rizzini *et al.* 2011; Liang *et al.* 2018; Lubobi Ferdinand *et al.* 2020)

As mentioned earlier, the UVR8-COP1 interaction stabilizes HY5, which, together with its homolog HYH, sequentially induces the activity of various transcription factors, thereby promoting the transcription of genes essential for secondary metabolite biosynthesis (Pandey *et al.* 2023b). Among these transcription factors, members of the WDR, bHLH, and MYB families are known to regulate the biosynthetic pathways of various secondary metabolites, including flavonoids, in multiple plant species. UVR8-mediated signaling can activate or inhibit the activity of key enzymes by regulating the expression of specific genes directly involved in secondary metabolic pathways, thereby affecting the synthesis and accumulation of secondary metabolites in medicinal plants. Research has shown that in *Arabidopsis thaliana*, HY5 can directly activate a set of R2R3-MYB transcription factor-encoding genes, such as MYB11, MYB12, and MYB111, which are responsible for the expression of several flavonoid biosynthesis genes, including CHI, CHS, and FLS1, under UV-B irradiation (Ralf *et al.* 2009). Yanjun *et al.* (2018) revealed that CmUVR8, COP1, and HY5 play pivotal roles in the expression of genes involved in the UV-B-mediated flavonoid biosynthesis pathway, thereby enhancing the accumulation of various flavonoids in the important medicinal plant *Chrysanthemum morifolium*. Numerous studies have indicated that UVR8 is upregulated following exposure to UV-B radiation, further influencing downstream signaling pathways related to UV-B perception. Conversely, Lubobi Ferdinand *et al.* (2020) found that under both short-term and long-term UV-B exposure, UVR8 is downregulated, and the transcription levels of transcription factors such as HY5, bHLH62, MYB4, and MYB12 (which regulate downstream structural genes) are affected to varying degrees. Moreover, the interaction of UVR8 signaling with other signaling pathways provides an additional layer for the fine regulation of secondary metabolism in medicinal plants. This interaction may involve plant hormone signaling pathways, thereby impacting the synthesis of secondary metabolites (Yang *et al.* 2020; Zhao *et al.* 2023).

UV-B Regulation of Secondary Metabolite Yield in Medicinal Plants

UV-B radiation, a significant component of the solar spectrum, exerts notable effects on the growth and metabolism of medicinal plants. In response to UV-B-imposed stress, these plants have evolved various strategies, including the synthesis of secondary metabolites (SMs), to mitigate stress effects (Schreiner *et al.* 2012; Lee *et al.* 2013; Kumari and Prasad 2013; Takshak and Agrawal 2019). Among these SMs, phenolic compounds, terpenoids, and alkaloids are essential components, closely associated with the plants' defensive mechanisms and pharmacological properties. Consequently, investigating the regulatory role of UV-B in the biosynthetic processes of SMs in medicinal plants remains a key area in botanical and pharmaceutical research. A substantial body of research has examined the effects of UV-B radiation on the biosynthesis of these SMs.

UV-B Regulation of Phenolic Secondary Metabolites

Phenolic compounds encompass a diverse group of plant chemicals characterized by at least one aromatic ring and a hydroxyl group, which endow them with varied biological activities (Balasundram *et al.* 2006). These compounds are central to physiological processes involving growth regulation, signal transduction, and responses to environmental stress (Zhang *et al.* 2021). Phenolic biosynthesis in plants occurs mainly through the mevalonate (MVA) and methylerythritol phosphate (MEP) pathways (Zagoskina *et al.* 2023). Notably, due to their antioxidant properties, polyphenols are central to the adaptive response of plants to UV-B radiation (Takshak and Agrawal 2019). For example, in highbush blueberry (*Vaccinium corymbosum*), phenolic compound levels increase under UV-B radiation, peaking after high UV-B doses and a 2-hour acclimatization period (Eichholz *et al.* 2011). Pandey *et al.* (2019) reported that UV-B exposure upregulates several phenolic and flavonoid compounds in *Artemisia annua*, with caffeic acid content rising 5.14-fold, accompanied by increases in chlorogenic acid, p-coumaric acid, coumarin, isoquercetin, luteolin-7-O-glucoside, caffeic acid lactone, rutin, quercetin, luteolin, and kaempferol. Additionally, Hu *et al.* (2020) showed that UV-B-induced expression of MdWRKY72 increases phenolic synthesis, particularly anthocyanins, by promoting MdMYB1 expression. Tumová and Tuma (2011) demonstrated that UV-B exposure affects isoflavonoid production in *Genista tinctoria*, significantly raising genistein, soy isoflavone, genistin, and biogenistin A levels. Furthermore, Luis *et al.* (2007) found that UV-B radiation notably increased the concentrations of rosmarinic acid and myristic acid in medicinal plants within the genus *Rosmarinus*.

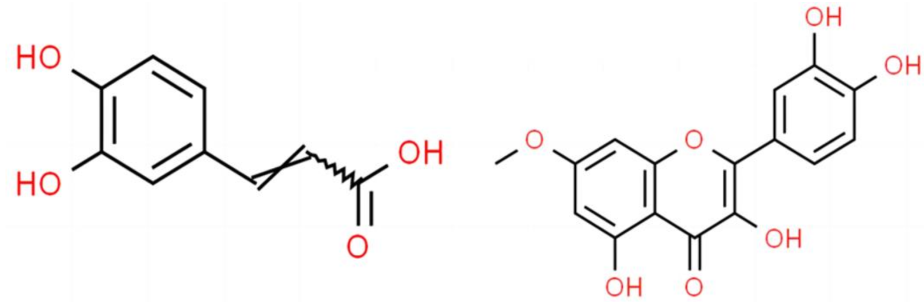

Fig. 2. Chemical structures of phenolic SMs: caffeic acid (left panel); rhamnetin (right panel)

UV-B Regulation of Terpenoid Secondary Metabolites

Terpenoids are a prevalent class of secondary metabolites, distinguished by their complex and diverse chemical structures, primarily composed of isoprene units (Bian *et al.* 2017). Terpenoids are classified into hemiterpenes through polyterpenes based on the number of isoprene units, exhibiting a diverse array of carbon skeletons (Bian *et al.* 2017).

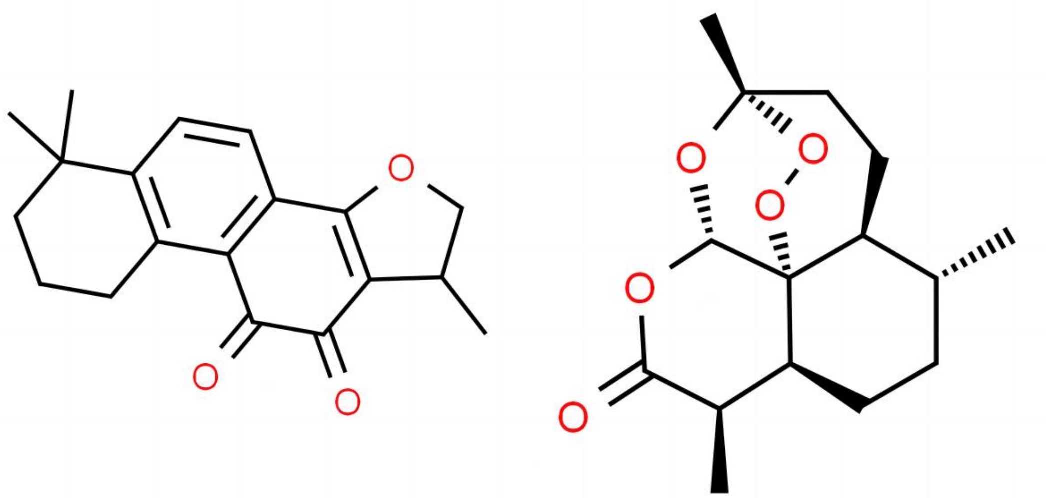

Fig. 3. Chemical structures of terpenoid SMs: cryptotanshinone (left panel); artemisinin (right panel)

Terpenoids are predominantly synthesized *via* the mevalonate (MVA) pathway or the 2-methylerythritol 4-phosphate (MEP) pathway, with isopentenyl pyrophosphate (IPP) and dimethylallyl pyrophosphate (DMAPP) acting as key direct precursors (Bian *et al.* 2017). Studies have demonstrated that UV-B radiation can promote the accumulation of terpenoids in multiple plant species (Takshak and Agrawal 2019). For instance, under enhanced UV-B (eUV-B) conditions, the accumulation of terpenoid secondary metabolites, including α-bergamotene, β-murrolene, β-farnesene, γ-turmerone, β-boswellic acid, and β-sesquiphellandrene, increases in *Curcuma longa* (Jaiswal and Agrawal 2021). Moreover, continuous UV-B exposure substantially increases the levels of terpenoid secondary metabolites in *Eclipta alba*, including α-terpineol and Δ-juniperene (Rai and Agrawal 2020). Under enhanced UV-B conditions, the yields of terpenoid secondary metabolites, such as β-zebranone, olivetol, pinanol, and 1,8-pinene, are also elevated in

Curcuma longa (Jaiswal *et al.* 2020). UV-B irradiation in *Coleus forskohlii* increases the content of terpenoid compounds, including isoprenol, trans-squalene, ganoderic acid A, β-carotene, and lycopene (Takshak and Agrawal 2015). Wang *et al.* (2016) confirmed that UV-B exposure enhances tanshinone accumulation in *Salvia miltiorrhiza* without inhibiting root growth.

UV-B Regulation of Alkaloid Secondary Metabolites

Alkaloids are nitrogen-containing organic compounds that play a significant role in plant defense mechanisms and are of considerable interest due to their diverse pharmacological activities (Zhang *et al.* 2021a; Zhang *et al.* 2021b). The biosynthesis of alkaloids involves a series of complex enzyme-catalyzed reactions, with amino acids such as tryptophan and phenylalanine typically serving as precursor molecules (Kishimoto *et al.* 2016). UV-B radiation has been identified as a key factor in promoting alkaloid biosynthesis, playing a crucial role in the synthesis of various alkaloids in medicinal plants. Takshak and Agrawal (2015) demonstrated that supplemental UV-B radiation (ambient radiation level + 0.042 W m^{-2}) increases alkaloid content in the leaves and roots of *Coleus forskohlii*. In *Clematis terniflora*, exposure to UV-B radiation (120.8 μW cm^{-2}), followed by incubation in darkness, was found to enhance indole alkaloid content by up to sevenfold (Gao *et al.* 2016). Additionally, a 6-hour UV-B treatment (1.208 W m^{-2}) of *Mahonia bealei* leaves, followed by incubation in darkness, significantly increased levels of protoberberine alkaloids, including berberine, palmatine, coptisine, and thalflavine (Zhang *et al.* 2014). In *Adhatoda vasica* Nees., exposure to enhanced UV-B (eUV-B) radiation resulted in increased levels of important quinazoline alkaloids, including vasicinone and vasicine (Pandey *et al.* 2021).

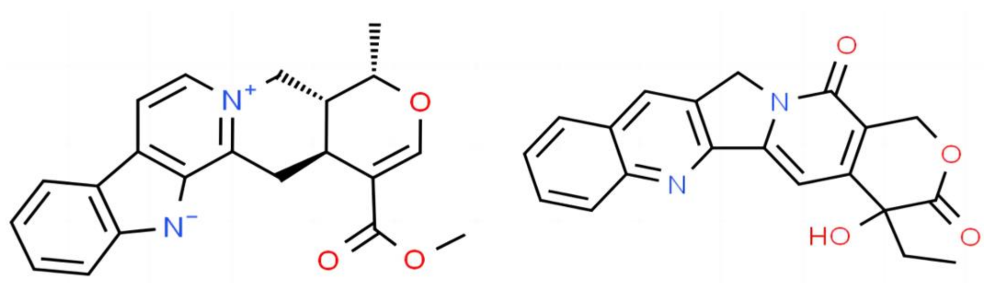

Fig. 4. Chemical structures of alkaloid SMs: serpentine (left panel); camptothecin (right panel)

Regulation of Secondary Metabolites by Different UV-B Conditions

The effects of UV-B radiation on medicinal plants vary significantly, depending on factors such as flux rate, duration, and wavelength (Ulm and Nagy 2005; Hectors *et al.* 2007; Jenkins 2009). This variability has led to investigations on how different UV-B intensities influence secondary metabolite (SM) production.

Table 1. Effect of UV-B on the Accumulation of SMs in Some Medicinal Plants

Type of SMs	Plant	UV-B treatment method	Change in SMs	References
Phenolics	Medicinal Plants of the Genus *Rosmarinus*	(0.063 and 0.359 W•m^{-2}), 14 d	Rosmarinic acid ↑	(Luis *et al.* 2007)
			Myristic acid ↑	
	Tropaeolum majus	(0.075 and 0.15 W•h•m^{-2}), 2 h and 22 h	Glucoside ↑	(Schreiner *et al.* 2009)
	Cymbopogon citratus	Higher than the environment (+1.8 and +3.6 kJ•m^{-2}•d^{-1}), 3 h•d^{-1}, Sustainable 80d	Flavonoids ↑	(Kumari and Agrawal 2010)
		0.150 W•h•m^{-2}, 2 h	Flavonoids ↑	(Eichholz *et al.* 2011)
			Phenolic acids ↑	
	Buckwheat Sprout	(890 W•m^{-2}), 24 h	Anthocyanins ↑	(Yoko *et al.* 2013)
			Rutin ↑	
	Bitter Lettuce	Intensity not mentioned 4 h•d^{-1}, Sustainable 3 d	Total flavonoids ↑	(Lee *et al.* 2013)
			Total phenolics ↑	
	Artemisia annua	(2.8 W•m^{-2}) 1 h, 2 h, 3 h, 4 h	Flavonoids ↑	(Pandey and Pandey-Rai 2014)
			Anthocyanins ↑	
	Withania somnifera	Environment (9.6 kJ•m^{-2}•d^{-1}) + Supplement (3.6 kJ•m^{-2}•d^{-1}), 3 h•d^{-1}, Sustainable 100 d	Flavonoids ↑	(Takshak and Agrawal 2014)
			Anthocyanins ↑	
	Prunella vulgaris	(35 μW•cm^{-2}•nm^{-1}), 30 min•d^{-1}, Sustainable 15 d	Total flavonoids ↑	(Zhang *et al.* 2017)
			Rosmarinic acid ↑	
			Caffeic acid ↑	
	Cymbopogon citratus	(Environment +7.2 kJ•m^{-2}•d^{-1}) 3 h•d^{-1}, Sustainable 110d	Total phenolics ↑	(Abdul *et al.* 2018)
			Tannins ↑	
	Perilla frutescens var. crispa	(0.05 W•m^{-2}) 3 h•d^{-1}, Sustained for 5 weeks	Rosmarinic acid ↑	(Yoshida *et al.* 2022)
	Salvia miltiorrhiza	(10.97 kJ•m^{-2}•d^{-1}) 1h•d^{-1}, Sustainable 5d	Total phenolics ↑	(Rizi *et al.* 2021)
			Flavonoids ↑	
Terpenoids	*Artemisia annua*	(4.2 kJ•m^{-2}•d^{-1}), 30 min•d^{-1}, Sustainable 14 d	Artemisinin ↑	(Rai *et al.* 2011)
		(0.4 W•m^{-2}),1 h•d^{-1}, Sustainable 10 d	Artemisinin ↑	(Pan *et al.* 2014)
	Salvia miltiorrhiza	(40 μW•cm^{-2}), 40 min	Total Danshen Keton ↑	(Wang *et al.* 2016)
			Cryptotanshinone ↑	
			Tanshinone I ↑	
			Tanshinone II A↑	
	Achyranthes bidentata	2 h (1.476 kJ•m^{-2}), 3 h (2.214 kJ•m^{-2}), 2 h and 3 h	Oleanolic acid ↑	(Li *et al.* 2019)
Alkaloids	*Withania somnifera*	Environment (9.6 kJ•m^{-2}•d^{-1})+ Supplementary (3.6 kJ•m^{-2}•d^{-1}), 3hd^{-1}, Sustainable 100 d	Total alkaloids ↑	(Takshak and Agrawal 2014)
			WithanolidesA↓	
	Fatsia japonica	(120.8 μW•cm^{-2}) 6h+ Dark cultivation	Berberine ↑	(Zhang *et al.* 2014)
			Palmitine ↑	
			Berberine ↑	

			Scopolamine ↑	
	Catharanthus roseus	(1345.00 μW•cm^{-2}), 1 h	Vincristine ↑	(Zhu *et al.* 2015)
			Arecoline ↑	
			Vincristine sulfate ↑	
	Clematis paniculata	(120.8 μW cm^{-2}), 5 h	Methyl (6-hydroxy-1H-indol-3-yl)carboxylate ↑	(Gao *et al.* 2016)

Note: "↑" indicates an increase in the corresponding secondary metabolites (SMs) of the medicinal plants, while "↓" indicates a decrease.

For instance, under low-density enhanced UV-B (3.2 kJ m^{-2} d^{-1}), saponin content, a major phytochemical in *Chlorophytum borivilianum*, increased by 26%. Chemical analysis of the roots revealed an increase in steroid components, including sterols and oleanolic acid, underscoring the role of low-density UV-B in stimulating medicinal compounds in this species(Jaiswal *et al.* 2023). Moreover, (Park *et al.* 2020) demonstrated that UV-B treatment (0.25 W m^{-2}) over four days enhanced antioxidant capacity, total hydroxycinnamic acids (HCAs), and several sesquiterpenoid compounds in *Crepidiastrum denticulatum*, without inhibiting growth. However, higher energy treatments (1.0 and 1.25 W m^{-2}) suppressed the fresh weight of young shoots. Takshak and Agrawal (2015) observed that supplemental UV-B increased secondary metabolite content in *Coleus forskohlii*, with leaves directly exposed to UV-B exhibiting higher levels of flavonoids and phenolic compounds. Conversely, (Jaiswal *et al.* 2020) reported that high-intensity UV-B exposure (ambient +/- 9.6 kJ m^{-2} d^{-1}) increased the production of certain sesquiterpenoids (such as curcumenol and β-caryophyllene) while decreasing others, including camphor and eucalyptol. Additionally, Pandey *et al.* (2021) found that high-intensity UV-B (enhanced UV-B; ambient +/- 7.2 kJ m^{-2} d^{-1}) treatment in *Adhatoda vasica* Nees. led to increased levels of triterpenoids, phytosterols, unsaturated fatty acids, diterpenes, tocopherols, and alkaloids, while reducing saturated fatty acids and sesquiterpenoids under enhanced UV-B conditions. These studies emphasize the complex regulation of various secondary metabolites in medicinal plants in response to varying UV-B radiation levels, highlighting the need for further exploration in this area.

Regulation of Secondary Metabolic Pathways by UV-B

UV-B radiation regulates secondary metabolite (SM) production by inducing the expression of genes involved in biosynthetic pathways at the transcriptional level (Apoorva *et al.* 2021). UVR8, the UV-B photoreceptor in plants, plays a critical role in sensing and transmitting UV-B signals, interacting with downstream transcription factors to mediate UV-B responses (Rizzini *et al.* 2011). In the model plant *Arabidopsis thaliana*, UVR8 has been shown to regulate the expression of more than 100 UV-B-responsive genes (Jenkins 2014). For instance, Eichholz *et al.* (2012) reported that quercetin-4'-O-glucoside, a flavonoid in *Asparagus officinalis*, increased with higher UV-B doses, accompanied by changes in the activity of polyphenol-related enzymes such as phenylalanine ammonia-lyase (PAL) and peroxidase. Zhang *et al.* (2018) found that UV-B radiation stimulated the expression of several genes involved in flavonoid biosynthesis in *Glycyrrhiza uralensis*, including cinnamate-4-hydroxylase (C4H), PAL, chalcone synthase (CHS), chalcone isomerase (CHI), and flavonol synthase (FLS). Supplemental UV-B significantly enhanced the activity of key enzymes such as PAL, cinnamate-4-hydroxylase (CAD), 4-coumarate ligase (4CL), CHI, and dihydroflavonol 4-reductase (DFR), leading to increased levels of flavonoids and phenolics in the leaves of *Coleus forskohlii* and *Withania somnifera* (Takshak and Agrawal 2014, 2015). Additionally, Inostroza-Blancheteau *et al.* (2014) reported that UV-B radiation differentially affected the expression of genes involved in the phenylpropanoid pathway in two cultivars of highbush blueberry (*Vaccinium corymbosum*, ‘Brigitta’ and ‘Bluegold’), including VcPAL, VcCHS, VcANS, VcF3'H, and VcMYBPA1. While many studies indicate that UV-B irradiation primarily upregulates genes involved in SM biosynthesis, some studies suggest that the effects may be inhibitory or minimal. For example, Pandey and Pandey-Rai (2014) observed that under 2.8 W m^{-2} UV-B radiation, genes in the artemisinin biosynthetic pathway (*e.g.*, HMGR, IPPi, DXR, ADS, CYP71AV1, FPS, and RED1) in *Artemisia annua* were upregulated, leading to significant accumulation of artemisinin. However, after 4 hours of UV-B treatment, genes encoding enzymes involved in synthesizing other sesquiterpenes, such as QHS, BFS, and ECS, were downregulated, while the transcription of the GAS gene did not show significant change. Similarly, after 16 hours of exposure to 4 W m^{-2} and 6 W m^{-2} UV-B, the expression of PAL, RAS, and TAT genes related to rosmarinic acid biosynthesis in *Perilla frutescens* was enhanced, resulting in increased rosmarinic acid levels. However, genes involved in anthocyanin biosynthesis (CHS, ANS, F3H, and DFR) exhibited decreased expression over 16-48 hours of UV-B exposure, leading to reduced anthocyanin levels (Yoshida *et al.* 2022). In *Bixa orellana*, UV-B radiation reduced the mRNA expression levels of genes involved in the biosynthesis of bixin (PSY, DXS, PDS, CMT, β-LCY, and ε-LCY), while mRNA levels of LCD and ADH were upregulated, with no significant changes in secondary pigments such as bixin and ABA (Sankari *et al.* 2017). Furthermore, Rodriguez-Morrison *et al.* (2021) reported that with increasing UV-B levels, the total cannabinoid concentration (THC and CBD) in cannabis inflorescences decreased, while the total terpene content varied by cultivar, indicating that UV-B radiation treatment does not optimize the composition of secondary metabolites in cannabis inflorescences.

Interaction of UV-B with Other Stresses

During the growth of medicinal plants, various environmental stresses are encountered, and the effect of one stressor may be exacerbated or mitigated by the presence of another. UV-B radiation can interact with other stress factors, potentially activating the plant's internal antioxidant system and promoting the accumulation of secondary metabolites. For instance, (Pandey *et al.* 2023a) reported that combined treatment with chromium (Cr) and UV-B resulted in the highest levels of psoralen (a furanocoumarin used in the treatment of psoriasis, vitiligo, and leucoderma) in the seeds of *Psoralea corylifolia*, while the chromium content in the seeds remained below the allowable limit. This suggests that *Psoralea corylifolia* can be cultivated in areas with high levels of UV-B and chromium pollution to optimize psoralen yield. Moreover, exposure to both UV-B and UV-A has been shown to enhance photosynthesis and increase flavonoid biosynthesis in medicinal plants, with changes also occurring in UV-B-induced phenolic compounds (Apoorva *et al.* 2021).

The interaction between UV-B radiation and water stress affects the plant’s water use efficiency and photosynthesis, resulting in varying impacts on the synthesis of secondary metabolites, such as flavonoids (Apoorva *et al.* 2021). Additionally, the combined effects of temperature and UV-B radiation may influence the production of secondary metabolites in medicinal plants. Low temperatures can exacerbate UV-B-induced oxidative stress, while high temperatures may inhibit certain secondary metabolic pathways. The specific impacts of UV-B radiation in combination with other stresses depend on the intensity, duration, and the plant’s adaptability to stress (Apoorva *et al.* 2021). However, the interaction of UV-B radiation with other environmental stress factors on secondary metabolite production in medicinal plants is complex. This complexity arises from factors such as plant species, stress intensity and duration, and fluctuations in environmental conditions. Therefore, further research is needed to better understand and utilize these interactions, revealing their potential molecular mechanisms and physiological processes.

DISCUSSION AND FUTURE RESEARCH DIRECTIONS

In the context of global environmental change, enhanced UV-B radiation has significantly impacted the secondary metabolites of plants, particularly medicinal plants. Investigating this impact in depth is crucial for the sustainable development and utilization of medicinal plant resources. By focusing on existing research, analyzing its limitations, considering multifactorial interactions, and exploring applications in agricultural practices, it is possible to improve the quality and yield of medicinal plants, thereby driving industry development.

Limitations in Research Scope

Currently, research on plants in the field of medicinal plants and secondary metabolites exhibits an uneven distribution. Most studies focus on specific medicinal plants and their secondary metabolites, such as the biosynthesis of artemisinin and flavonoids, which have attracted considerable attention. However, exploration of many other plants and their metabolites remains relatively insufficient (Li *et al.* 2021). On the one hand, there is a significant limitation in the scope of plant species studied; widely researched plants dominate, while many underexplored medicinal plants, especially rare species with restricted distribution and unique habitats, such as *Dendrobium* spp. and *Saussurea involucrata*, urgently need to be included in research efforts (Gong and Zheng 2021; Long *et al.* 2023). At the secondary metabolite level, while traditional focuses such as alkaloids, terpenoids, and phenolics are well-established, other key metabolites such as polysaccharides, organic acids, and volatile oils also warrant attention. Polysaccharides have potential mechanisms in plant immune regulation and antioxidant stress (Chen and Huang 2019); organic acids may serve as critical signaling molecules in plant stress adaptation and microbial interactions (Nakata *et al.* 2000); and volatile oils hold tremendous potential in plant communication and ecological regulation (Kumari *et al.* 2014). However, studies on the impact of changes in their synthesis and release patterns on ecological relationships are limited. Research on the molecular mechanisms underlying UV-B radiation's impact on the secondary metabolites of medicinal plants remains incomplete, requiring a deeper understanding of how UV-B regulates the synthesis of secondary metabolites through gene expression and enzyme activity modulation. Comparative studies using model plants (*e.g.*, *Arabidopsis thaliana*) and non-model medicinal plants could elucidate the unique molecular mechanisms of medicinal plants in response to UV-B radiation. Additionally, the role of plant hormone analogs in UV-B responses deserves more attention. Although a few studies have focused on specific analogs, such as gibberellins (Ma *et al.* 2020), most hormone analogs lack systematic analysis regarding their roles and associations within the UV-B signal transduction network. For instance, the molecular details of cytokinin analogs in regulating secondary metabolite synthesis remain unclear. Genomics, metabolomics, and proteomics approaches could further unravel how UV-B influences gene expression and metabolic pathways in medicinal plants. Finally, medicinal plants from diverse ecological types, such as those from arid regions producing osmotic regulators such as betaine (Wang *et al.* 2019), or halophytes enriched with unique salt-tolerant secondary metabolites like proline, betaine, and coumarinol (Gao *et al.* 2022), merit greater attention. These secondary metabolites, generated under extreme conditions, not only have extraordinary medicinal value but also hold profound significance for ecological research.

Multi-factorial Considerations

When studying the effects of UV-B radiation on the secondary metabolites of medicinal plants, it is crucial to consider multiple factors comprehensively. First, significant differences in experimental design and methodology arise due to variations in research subjects. Studies often select different medicinal plants, leading to a lack of standardization in key experimental procedures. Regarding UV-B radiation, parameters such as intensity, duration, dosage, and frequency vary widely. Similarly, the methods used for extracting and analyzing secondary metabolites differ, resulting in disparate outcomes. Some studies report that UV-B radiation increases the content of certain secondary metabolites in medicinal plants, while others suggest minimal or even negative effects, making cross-comparison of results highly challenging (Pandey and Pandey-Rai 2014). To enhance the credibility and comparability of research findings, it is essential to standardize certain aspects of experimental design. Specifically, parameters such as UV-B radiation dosage, exposure time, and frequency should be normalized to facilitate cross-laboratory comparisons. Additionally, consistent use of advanced analytical techniques, such as ultra-high-performance liquid chromatography (UHPLC), high-performance liquid chromatography (HPLC), and gas chromatography-mass spectrometry (GC-MS), can improve result accuracy. Moreover, most current studies overlook the interactions between UV-B radiation and other environmental factors. Variables such as temperature, water availability, soil type, microorganisms, and pH conditions may interfere with the effects of UV-B radiation on secondary metabolites (Paajanen *et al.* 2011; Kharel *et al.* 2023). Future research should prioritize experimental designs that explore these complex interactions in depth to advance the development of this field.

Applications in Agricultural Practices

Within the current research framework on the effects of UV-B radiation on medicinal plants, translating research findings into agricultural practices represents a promising and necessary direction for exploration.

On the one hand, cultivar selection holds significant importance. Precisely identifying medicinal plant cultivars that exhibit favorable responses to UV-B radiation is the first step, requiring rigorous experimental support. Beyond enhancing secondary metabolite content, it is essential to comprehensively evaluate a cultivar's adaptability and stress resistance to ensure robust growth in complex and dynamic natural and agricultural environments. For instance, certain medicinal plants from high-altitude regions, having undergone long-term natural selection, possess unique tolerance to intense UV-B radiation. Uncovering such traits can provide new insights for cultivar breeding (Sedej *et al.* 2020; Terfa *et al.* 2014). On the other hand, modern biotechnologies offer innovative tools. Utilizing transgenic and gene-editing technologies to develop new cultivars with enhanced responses to UV-B radiation has the potential to overcome traditional cultivation bottlenecks (Liu *et al.* 2020). However, this process must be accompanied by rigorous ecological risk assessments to prevent potential adverse consequences such as biological invasions and genetic contamination, thereby safeguarding ecosystem authenticity and stability.

Furthermore, integrating agricultural practice strategies is essential. UV-B regulation can be organically combined with light quality control, stress management, and soil improvement to construct comprehensive management plans. For example, intercropping or crop rotation schemes can strategically pair plants with varying UV-B responses, optimizing light resource allocation, stimulating the accumulation of secondary metabolites, and maintaining soil fertility. Simultaneously, the rational use of covering measures, such as shading nets and mulching films, can precisely modulate UV-B radiation intensity, creating a favorable microenvironment for medicinal plants. These measures also reduce soil erosion, suppress water evaporation, and enhance productivity and quality while preserving biodiversity, advancing the medicinal plant industry toward sustainable development. Future research should adhere to standardized and systematic principles, expand research boundaries, and delve deeper into molecular mechanisms and practical application potential.

CONCLUSIONS

UV-B radiation, as an environmental stressor, has a notable influence on the secondary metabolites of medicinal plants. A synthesis of past studies reveals that the regulatory processes affecting the metabolome of medicinal plants under UV-B radiation are highly intricate and influenced by multiple factors, including plant species, genotype, growth stage, UV-B radiation dynamics, and various environmental conditions. Upon exposure to UV-B radiation, internal signal transduction pathways in plants are activated, thereby promoting the biosynthesis of secondary metabolites. These findings not only enhance our understanding of the adaptive responses of plants but also pave new pathways for improving the medicinal value of plants. Nevertheless, there remain significant gaps in current research. Future efforts must adopt multidisciplinary approaches to explore the following aspects in depth.

It is critical to elucidate how secondary metabolites are synthesized in plants under UV-B irradiation and how these metabolites contribute to photoprotection. Such insights could support the development of novel methods to enhance plant resistance to ultraviolet radiation, such as the precise regulation of biosynthetic pathways through genetic engineering (D’Orso *et al.* 2023). Secondly, Investigate the interaction mechanisms between secondary metabolites and UV-activated chemical substances. Research should aim to determine the specific ways in which secondary metabolites alleviate potential damage, including their binding patterns, metabolic pathways, and impacts on cellular signal transduction.

Proteomics technology offers substantial potential in this field. For instance, studies on *Catharanthus roseus* and *Mahonia bealei* have demonstrated significant alterations in phosphorylated proteins under UV-B radiation, primarily involving key processes such as protein synthesis, modification, degradation, and signal transduction (Liu *et al.* 2022; Zhong *et al.* 2019). A thorough analysis of the functions of these altered proteins can provide critical insights into the signaling and metabolic regulatory pathways in plants exposed to UV-B radiation. Complementary molecular biology techniques, such as qRT-PCR, can be utilized to detect changes in gene expression, further verifying proteomic findings at the mRNA level. This integrated approach enables a comprehensive understanding of gene regulatory mechanisms.

Moreover, it is essential to integrate these advanced insights into agricultural practices. By leveraging the interactions between UV-B radiation and secondary metabolites, precision agriculture technologies can be developed to optimize the cultivation conditions for medicinal plants. Interdisciplinary collaborations that merge biology, agronomy, pharmacology, and ecology are indispensable for the sustainable utilization of medicinal plants and the conservation of biodiversity. In-depth elucidation of the interaction mechanisms between UV-B radiation and secondary metabolites will undoubtedly open new horizons in the research and application of medicinal plants. This advancement will propel the industry toward stable and sustainable development amidst the challenges posed by global environmental changes.

REFERENCES CITED

Abdul, H., Suruchi, S., Madhoolika, A., and Shashi Bhushan, A. (2018). "*Heteropogon contortus* BL-1 (pilli grass) and elevated UV-B radiation: The role of growth, physiological, and biochemical traits in determining forage productivity and quality," *Photochem Photobiol* 95(2), article 12990. DOI: 10.1111/php.12990

Apoorva, Jaiswal, D., Pandey-Rai, S., and Agrawal, S. B. (2021). "Untangling the UV-B radiation-induced transcriptional network regulating plant morphogenesis and secondary metabolite production," *Environmental and Experimental Botany* 192, article 104655. DOI: 10.1016/j.envexpbot.2021.104655

Balasundram, N., Sundram, K., and Samman, S. (2006). "Phenolic compounds in plants and agri-industrial by-products: Antioxidant activity, occurrence, and potential uses," *Food Chemistry* 99(1), 191-203. DOI: 10.1016/j.foodchem.2005.07.042

Bian, G., Deng, Z., and Liu, T. (2017). "Strategies for terpenoid overproduction and new terpenoid discovery," *Curr Opin Biotechnol* 48, 234-241. DOI: 10.1016/j.copbio.2017.07.002

Chen, F., and Huang, G. (2019). "Antioxidant activity of polysaccharides from different sources of ginseng," *International Journal of Biological Macromolecules* 125, 906-908. DOI: 10.1016/j.ijbiomac.2018.12.134

D'Orso, F., Hill, L., Appelhagen, I., Lawrenson, T., Possenti, M., Li, J., Harwood, W., Morelli, G., and Martin, C. (2023). "Exploring the metabolic and physiological roles of HQT in *S. lycopersicum* by gene editing, *Frontiers in Plant Science* 14, article 1124959. DOI: 10.3389/fpls.2023.1124959.

Eichholz, I., Huyskens-Keil, S., Keller, A., Ulrich, D., Kroh, L. W., and Rohn, S. (2011). "UV-B-induced changes of volatile metabolites and phenolic compounds in blueberries (*Vaccinium corymbosum* L.)." *Food Chemistry* 126(1), 60-64. DOI: 10.1016/j.foodchem.2010.10.071

Eichholz, I., Rohn, S., Gamm, A., Beesk, N., Herppich, W. B., Kroh, L. W., Ulrichs, C., and Huyskens-Keil, S. (2012). "UV-B-mediated flavonoid synthesis in white asparagus (*Asparagus officinalis* L.)." *Food Res. Int*. 48(1), 196-201. DOI: 10.1016/j.foodres.2012.03.008

Fang, F., Lin, L., Zhang, Q. W., Lu, M., Skvortsova, M. Y., Podolec, R., Zhang, Q. Y., Pi, J. H., Zhang, C. L., Ulm, R., and Yin, R. H. (2022). "Mechanisms of UV-B light-induced photoreceptor UVR8 nuclear localization dynamics," *New Phytol*. 236(5), 1824-1837. DOI: 10.1111/nph.18468

Gao, C., Yang, B., Zhang, D., Chen, M., and Tian, J. (2016). "Enhanced metabolic process to indole alkaloids in *Clematis terniflora* DC. after exposure to high level of UV-B irradiation followed by the dark," *BMC Plant Biology* 16(1), article 231. DOI: 10.1186/s12870-016-0920-3

Gao, Y., Jin, Y., Guo, W., Xue, Y., and Yu, L. (2022). "Metabolic and physiological changes in the roots of two oat cultivars in response to complex saline-alkali stress," *Frontiers in Plant Science* 13, article 835414. DOI: 10.3389/fpls.2022.835414

Gong, G., and Zheng, Y. (2021). "The anti-UV properties of *Saussurea involucrate* Matsum. & Koidz. *via* regulating PI3K/Akt pathway in B16F10 cells," *Journal of Ethnopharmacology*, 269, 113694. DOI: 10.1016/j.jep.2020.113694

Hectors, K., Prinsen, E., de Coen, W., Jansen, M. A. K., and Guisez, Y. (2007). "*Arabidopsis thaliana* plants acclimated to low dose rates of ultraviolet B radiation show specific changes in morphology and gene expression in the absence of stress symptoms," *New Phytol*. 175. DOI: 10.1111/j.1469-8137.2007.02092.x

Hu, J. F., Fang, H. C., Wang, J., Yue, X. X., Su, M. Y., Mao, Z. L., Zou, Q., Jiang, H. Y., Guo, Z. W., Yu, L., Feng, T., Lu, L., Peng, Z. G., Zhang, Z. Y., Wang, N., and Chen, X. S. (2020). "Ultraviolet B-induced MdWRKY72 expression promotes anthocyanin synthesis in apple," *Plant Sci*. 292, article 110377. DOI: 10.1016/j.plantsci.2019.110377

Inostroza-Blancheteau, C., Reyes-Díaz, M., Arellano, A., Latsague, M., Acevedo, P., Loyola, R., Arce-Johnson, P., and Alberdi, M. (2014). "Effects of UV-B radiation on anatomical characteristics, phenolic compounds and gene expression of the phenylpropanoid pathway in highbush blueberry leaves," *Plant Physiol. Bioch*. 85, 85-95. DOI: 10.1016/j.plaphy.2014.10.015

Jaiswal, D., and Agrawal, S. B. (2021). "Ultraviolet-B induced changes in physiology, phenylpropanoid pathway, and essential oil composition in two *Curcuma* species (*C. caesia* Roxb. and *C. longa* L.)." *Ecotox. Environ. Safe* 208, article 111739. DOI: 10.1016/j.ecoenv.2020.111739

Jaiswal, D., Pandey, A., Agrawal, M., and Agrawal, S. B. (2023). "Photosynthetic, biochemical and secondary metabolite changes in a medicinal plant *Chlorophytum borivillianum* (Safed musli) against low and high doses of UV-B radiation," *Photochemistry and Photobiology* 99(1), 45-56. DOI: 10.1111/php.13672

Jaiswal, D., Pandey, A., Mukherjee, A., Agrawal, M., and Agrawal, S. B. (2020). "Alterations in growth, antioxidative defense and medicinally important compounds of *Curcuma caesia* Roxb. under elevated ultraviolet-B radiation," *Environmental and Experimental Botany* 177, article 104152. DOI: 10.1016/j.envexpbot.2020.104152

Jenkins, G. I. (2009). "Photomorphogenic UV-B perception and signal transduction in *Arabidopsis*," *Comp. Biochem. Phys. A*, 153a(2), S203-S203. DOI: 10.1016/j.cbpa.2009.04.638

Jenkins, G. I. (2014). "The UV-B photoreceptor UVR8: From structure to physiology," *Plant Cell* 26(1), 21-37. DOI: 10.1105/tpc.113.119446

Kharel, B., Rusalepp, L., Bhattarai, B., Kaasik, A., Kupper, P., Lutter, R., Mänd, P., Rohula-Okunev, G., Rosenvald, K., and Tullus, A. (2023). "Effects of air humidity and soil moisture on secondary metabolites in the leaves and roots of *Betula pendula* of different competitive status," *Oecologia* 202(2), 193-210. DOI: 10.1007/s00442-023-05388-9

Kishimoto, S., Sato, M., Tsunematsu, Y., and Watanabe, K. (2016). "Evaluation of biosynthetic pathway and engineered biosynthesis of alkaloids," *Molecules* 21(8), article 1078. DOI: 10.3390/molecules21081078

Kumari, R., and Agrawal, S. (2010). "Supplemental UV‐B induced changes in leaf morphology, physiology and secondary metabolites of an Indian aromatic plant *Cymbopogon citratus* (DC) Staph under natural field conditions," *International Journal of Environmental Studies* 67(5), 655-675. DOI: 10.1080/00207233.2010.513828

Kumari, R., and Prasad, M.N.V. (2013). "Medicinal plant active compounds produced by UV-B exposure," in: *Sustainable Agriculture Reviews* vol. 12, E. Lichtfouse (ed.), Springer, Dordrecht.

Kumari, S., Pundhir, S., Priya, P., Jeena, G., Punetha, A., Chawla, K., Firdos Jafaree, Z., Mondal, S., and Yadav, G. (2014). "EssOilDB: A database of essential oils reflecting terpene composition and variability in the plant kingdom," *Database*, 2014. DOI: 10.1093/database/bau120

Lee, M.-J., Son, J. E., and Oh, M.-M. (2013). "Growth and phenolic content of sowthistle grown in a closed-type plant production system with a UV-A or UV-B lamp," *Horticulture, Environment, and Biotechnology* 54(6), 492-500. DOI: 10.1007/s13580-013-0097-8

Li, J., Han, X., Wang, C., Tang, L., Zhang, W., and Qi, W. (2019). "The response of *Achyranthes bidentata* Blume to short-term UV-B exposure," *Russian Journal of Plant Physiology* 66(1), 160-170. DOI: 10.1134/S1021443719010096

Li, Y., Qin, W., Fu, X., Zhang, Y., Hassani, D., Kayani, S.-I., Xie, L., Liu, H., Chen, T., Yan, X., Peng, B., Wu-Zhang, K., Wang, C., Sun, X., Li, L., and Tang, K. (2021). "Transcriptomic analysis reveals the parallel transcriptional regulation of UV-B-induced artemisinin and flavonoid accumulation in *Artemisia annua* L," *Plant Physiol Bioch*. 163, 189-200. DOI: 10.1016/j.plaphy.2021.03.052

Liang, T., Yang, Y., and Liu, H. T. (2018). "Signal transduction mediated by the plant UV-B photoreceptor UVR8," *New Phytol*. 221(3), 1247-1252. DOI: 10.1111/nph.15469

Liaqat, W., Altaf, M. T., Barutcular, C., Nawaz, H., Ullah, I., Basit, A., and Mohamed, H. I. (2024). "Ultraviolet-B radiation in relation to agriculture in the context of climate change: A review," *Cereal Res. Commun*. 52(1), 1-24. DOI: 10.1007/s42976-023-00375-5

Lin, L., Dong, H. X., Yang, G. Q., and Yin, R. H. (2020). "The C-terminal 17 amino acids of the photoreceptor UVR8 is involved in the fine-tuning of UV-B signaling," *J. Integr. Plant Biol*. 62(9), 1327-1340. DOI: 10.1111/jipb.12977

Liu, A., Liu, S., Li, Y., Tao, M., Han, H., Zhong, Z., Zhu, W., and Tian, J. (2022). "Phosphoproteomics reveals regulation of secondary metabolites in *Mahonia bealei* exposed to ultraviolet-B radiation," *Frontiers in Plant Science* 12, article 794906. DOI: 10.3389/fpls.2021.794906

Liu, X., Zhang, Q., Yang, G., Zhang, C., Dong, H., Liu, Y., Yin, R., and Lin, L. (2020). "Pivotal roles of tomato photoreceptor SlUVR8 in seedling development and UV-B stress tolerance," *Biochemical and Biophysical Research Communications* 522(1), 177-183. DOI: 10.1016/j.bbrc.2019.11.073

Long, Y., Wang, W., Zhang, Y., Du, F., Zhang, S., Li, Z., Deng, J., and Li, J. (2023). "Photoprotective effects of *Dendrobium nobile* Lindl. polysaccharides against UVB-induced oxidative stress and apoptosis in HaCaT Cells," *International Journal of Molecular Sciences* 24(7), article 6120. DOI: 10.3390/ijms24076120

Lubobi Ferdinand, S., Han-Chen, Z., Zhuo-Xiao, H., and Shu, W. (2020). "UV-B induces distinct transcriptional re-programing in UVR8-signal transduction, flavonoid, and terpenoids pathways in *Camellia sinensis*," *Front. Plant Sci*. 11(0), article 234. DOI: 10.3389/fpls.2020.00234

Luis, J. C., Pérez, R. M., and González, F. V. (2007). "UV-B radiation effects on foliar concentrations of rosmarinic and carnosic acids in rosemary plants," *Food Chemistry*, 101(3), 1211-1215. DOI: 10.1016/j.foodchem.2006.03.023

Ma, T., Gao, H., Zhang, D., Shi, Y., Zhang, T., Shen, X., Wu, L., Xiang, L., and Chen, S. (2020). "Transcriptome analyses revealed the ultraviolet B irradiation and phytohormone gibberellins coordinately promoted the accumulation of artemisinin in *Artemisia annua* L," *Chinese Medicine* 15(1), article 67. DOI: 10.1186/s13020-020-00344-8

Munasira Begum, V. S., Mohamed Tariq, N. P. M. T. N. P. M., H, J., and Muhammed Shariq, K. (2022). "Plants secondary metabolites as medicines: A review," *International Journal of Zoological Investigations* 18(1), 490-493. DOI: 10.33745/ijzi.2022.v08i01.056

Nakata, K., Kobayashi, T., Takiguchi, Y., and Yamaguchi, T. (2000). "Regulation by organic acids of polysaccharide-mediated microbe-plant interactions," *Bioscience, Biotechnology, and Biochemistry* 64(10), 2040-2046. DOI: 10.1271/bbb.64.2040

Paajanen, R., Julkunen-Tiitto, R., Nybakken, L., Petrelius, M., Tegelberg, R., Pusenius, J., Rousi, M., and Kellomäki, S. (2011). "Dark-leaved willow (*Salix myrsinifolia*) is resistant to three-factor (elevated CO_2, temperature and UV-B-radiation) climate change," *New Phytol*. 190(1), 161-168. DOI: 10.1111/j.1469-8137.2010.03583.x

Pan, W., Zheng, L., Tian, H., Li, W., and Wang, J. (2014). "Transcriptome responses involved in artemisinin production in *Artemisia annua* L. under UV-B radiation," *Journal of Photochemistry and Photobiology. B, Biology* 140, 292-300. DOI: 10.1016/j.jphotobiol.2014.08.013

Pandey, N., and Pandey-Rai, S. (2014). "Short term UV-B radiation-mediated transcriptional responses and altered secondary metabolism of in vitro propagated plantlets of *Artemisia annua* L.," *Plant Cell, Tissue and Organ Culture (PCTOC)*, 116(3), 371-385. DOI: 10.1007/s11240-013-0413-0

Pandey, N., Goswami, N., Tripathi, D., Rai, K. K., Rai, S. K., Singh, S., and Pandey-Rai, S. (2019). "Epigenetic control of UV-B-induced flavonoid accumulation in *Artemisia annua* L." *Planta* 249(2), 497-514. DOI: 10.1007/s00425-018-3022-7

Pandey, A., Jaiswal, D., and Agrawal, S. B. (2021). "Ultraviolet-B mediated biochemical and metabolic responses of a medicinal plant *Adhatoda vasica* Nees. at different growth stages," *J Photoch Photobio B*, 216. DOI: 10.1016/j.jphotobiol.2021.112142

Pandey, A., Agrawal, M., and Agrawal, S. B. (2023a). "Individual and combined effects of chromium and ultraviolet-B radiation on defense system, ultrastructural changes, and production of secondary metabolite psoralen in a medicinal plant *Psoralea corylifolia* L," *Environmental Science and Pollution Research* 30(2), 4372-4385. DOI: 10.1007/s11356-022-22480-4

Pandey, A., Agrawal, M., and Agrawal, S. B. (2023b). "Ultraviolet-B and heavy metal-induced regulation of secondary metabolites in medicinal plants: A review," *Metabolites* 13(3). DOI: 10.3390/metabo13030341

Park, S. Y., Lee, M. Y., Lee, C. H., and Oh, M. M. (2020). "Physiologic and metabolic changes in *Crepidiastrum denticulatum* according to different energy levels of UV-B radiation," *International Journal of Molecular Sciences* 21(19). DOI: 10.3390/ijms21197134

Podolec, R., Demarsy, E., and Ulm, R. (2021). "Perception and signaling of ultraviolet-B radiation in plants," *Annu. Rev. Plant Biol*. 72, 793-822. DOI: 10.1146/annurev-arplant-050718-095946

Rai, K., and Agrawal, S. B. (2020). "Effect on essential oil components and wedelolactone content of a medicinal plant Eclipta alba due to modifications in the growth and morphology under different exposures of ultraviolet-B," *Physiol. Mol.*

Biol. Pla. 26(4), 773-792. DOI: 10.1007/s12298-020-00780-8

Rai, R., Meena, R., Smita, S., Shukla, A., Rai, S., and Pandey-Rai, S. (2011). "UV-B and UV-C pre-treatments induce physiological changes and artemisinin biosynthesis in *Artemisia annua* L. - an antimalarial plant," *Journal of Photochemistry and Photobiology. B, Biology* 105(3), 216-225. DOI: 10.1016/j.jphotobiol.2011.09.004

Ralf, S., Jean-Jacques, F., Henriette, G., Lutz, B., Sebastian, B., Melanie, B., Markus, F., Bernd, W., and Roman, U. (2009). "The *Arabidopsis* bZIP transcription factor HY5 regulates expression of the PFG1/MYB12 gene in response to light and ultraviolet-B radiation," *Plant Cell Environ*, 33(1). DOI: 10.1111/j.1365-3040.2009.02061.x

Rizi, M. R., Azizi, A., Sayyari, M., Mirzaie-Asl, A., and Conti, L. (2021). "Increased phenylpropanoids production in UV-B irradiated *Salvia verticillata* as a consequence of altered genes expression in young leaves," *Plant Physiol. Bioch*. 167, 174-184. DOI: 10.1016/j.plaphy.2021.07.037

Rizzini, L., Favory, J.-J., Cloix, C., Faggionato, D., O'Hara, A., Kaiserli, E., Baumeister, R., Schäfer, D., Nagy, F., Jenkins, G., and Ulm, R. (2011). "Perception of UV-B by the *Arabidopsis* UVR8 protein," *Science* 332(6025), 103-106. DOI: 10.1126/science.1200660

Rodriguez-Morrison, V., Llewellyn, D., and Zheng, Y.-B. (2021). "*Cannabis* inflorescence yield and cannabinoid concentration are not increased with exposure to short-wavelength ultraviolet-B radiation," *Front. Plant Sci*. 12, article 725078. DOI: 10.3389/fpls.2021.725078

Sankari, M., Hridya, H., Sneha, P., Doss, C. G. P., and Ramamoorthy, S. (2017). "Effect of UV radiation and its implications on carotenoid pathway in *Bixa orellana* L," *J. Photoch. Photobio. B*, 176, 136-144. DOI: 10.1016/j.jphotobiol.2017.10.002

Schreiner, M., Krumbein, A., Mewis, I., Ulrichs, C., and Huyskens-Keil, S. (2009). "Short-term and moderate UV-B radiation effects on secondary plant metabolism in different organs of nasturtium (*Tropaeolum majus* L.)." *Innovative Food Science & Emerging Technologies* 10(1), 93-96. DOI: 10.1016/j.ifset.2008.10.001

Schreiner, M., Mewis, I., Huyskens-Keil, S., Jansen, M. A. K., Zrenner, R., Winkler, J. B., O'Brien, N., and Krumbein, A. (2012). "UV-B-induced secondary plant metabolites - Potential benefits for plant and human health," *Crit. Rev. Plant Sci*. 31(3), 229-240. DOI: 10.1080/07352689.2012.664979

Sedej, T. T., Erznožnik, T., and Rovtar, J. (2020). "Effect of UV radiation and altitude characteristics on the functional traits and leaf optical properties in *Saxifraga hostii* at the alpine and montane sites in the Slovenian Alps," *Photochemical & Photobiological Sciences* 19(2), 180-192. DOI: 10.1039/c9pp00032a

Song, Y., Ma, B., Guo, Q., Zhou, L., Zhou, X., Ming, Z., You, H., and Zhang, C. (2023). "MYB pathways that regulate UV-B-induced anthocyanin biosynthesis in blueberry (*Vaccinium corymbosum*)," *Frontiers in Plant Science* 14, article 1125382. DOI: 10.3389/fpls.2023.1125382

Takshak, S., and Agrawal, S. B. (2014). "Secondary metabolites and phenylpropanoid pathway enzymes as influenced under supplemental ultraviolet-B radiation in *Withania somnifera* Dunal, an indigenous medicinal plant," *J. Photoch. Photobio. B* 140, 332-343. DOI: 10.1016/j.jphotobiol.2014.08.011

Takshak, S., and Agrawal, S. B. (2014). "Secondary metabolites and phenylpropanoid pathway enzymes as influenced under supplemental ultraviolet-B radiation in *Withania somnifera* Dunal, an indigenous medicinal plant," *Journal of Photochemistry and Photobiology. B, Biology* 140, 332-343. DOI:

10.1016/j.jphotobiol.2014.08.011
Takshak, S., and Agrawal, S. B. (2015). "Defence strategies adopted by the medicinal plant *Coleus forskohlii* against supplemental ultraviolet-B radiation: Augmentation of secondary metabolites and antioxidants," *Plant Physiol. Bioch*. 97, 124-138. DOI: 10.1016/j.plaphy.2015.09.018
Takshak, S., and Agrawal, S. B. (2019). "Defense potential of secondary metabolites in medicinal plants under UV-B stress," *Journal of Photochemistry and Photobiology B-Biology* 193, 51-88. DOI: 10.1016/j.jphotobiol.2019.02.002
Terfa, M. T., Roro, A. G., Olsen, J. E., and Torre, S. (2014). "Effects of UV radiation on growth and postharvest characteristics of three pot rose cultivars grown at different altitudes," *Scientia Horticulturae* 178, 184-191. DOI: 10.1016/j.scienta.2014.08.021
Thakur, M., Bhattacharya, S., Khosla, P., and Puri, S. (2019). "Improving production of plant secondary metabolites through biotic and abiotic elicitation," *Journal of Applied Research on Medicinal and Aromatic Plants* 12, 1-12. DOI: 10.1016/J.JARMAP.2018.11.004
Tumová, L., and Tuma, J. (2011). "The effect of UV light on isoflavonoid production in *Genista tinctoria* culture *in vitro*," *Acta Physiol. Plant*. 33(2), 635-640. DOI: 10.1007/s11738-010-0566-y
Ulm, R., and Nagy, F. (2005). "Signalling and gene regulation in response to ultraviolet light," *Current Opinion in Plant Biology* 8(5), 477-482. DOI: 10.1016/j.pbi.2005.07.004
Wang, C., Zheng, L., Tian, H., and Wang, J. (2016). "Synergistic effects of ultraviolet-B and methyl jasmonate on tanshinone biosynthesis in *Salvia miltiorrhiza* hairy roots," *Journal of Photochemistry and Photobiology. B, Biology* 159, 93-100. DOI: 10.1016/j.jphotobiol.2016.01.012
Wang, N., Cao, F., Richmond, M. E. A., Qiu, C., and Wu, F. (2019). "Foliar application of betaine improves water-deficit stress tolerance in barley (*Hordeum vulgare* L.)." *Plant Growth Regulation* 89(1), 109-118. DOI: 10.1007/s10725-019-00510-5
Wargent, J., and Paul, N. (2007). "Mechanisms of response to ultraviolet-b radiation — A whole plant perspective," *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* 146(4, Supplement), S228. DOI: 10.1016/j.cbpa.2007.01.502
Wink, M. (2015). "Modes of action of herbal medicines and plant secondary metabolites," *Medicines* 2, 251-286. DOI: 10.3390/medicines2030251
Wong, H. J., Mohamad-Fauzi, N., Rizman-Idid, M., Convey, P., and Alias, S. A. (2019). "Protective mechanisms and responses of micro-fungi towards ultraviolet-induced cellular damage," *Polar Sci*. 20, 19-34. DOI: 10.1016/j.polar.2018.10.001
Yang, B., Tang, J., Yu, Z. H., Khare, T., Srivastav, A., Datir, S., and Kumar, V. (2019). "Light stress responses and prospects for engineering light stress tolerance in crop plants," *J. Plant Growth Regul*. 38(4), 1489-1506. DOI:10.1007/s00344-019-09951-8
Yang, Y., Zhang, L. B., Chen, P., Liang, T., Li, X., and Liu, H. T. (2020). "UV-B photoreceptor UVR8 interacts with MYB73/MYB77 to regulate auxin responses and lateral root development," *Embo J*. 39(2). DOI: 10.15252/embj.2019101928
Yanjun, Y., Xiuli, Y., Zhifang, J., Zhehao, C., Xiujun, R., Weiyang, J., Ying, W., Xiaojing, S., and Maojun, X. (2018). "UV resistance locus 8 from *Chrysanthemum morifolium* Ramat (CmUVR8) plays important roles in UV-B signal transduction and UV-B-Induced accumulation of flavonoids," *Front. Plant Sci*. 9(0), article 955. DOI: 10.3389/fpls.2018.00955

Yeshi, K., Crayn, D., Ritmejeryte, E., and Wangchuk, P. (2022). "Plant secondary metabolites produced in response to abiotic stresses has potential application in pharmaceutical product development," *Molecules* 27, article 27010313. DOI: 10.3390/molecules27010313

Yoko, T., Tetsuya, T., Takuya, K., Akihide, K., Osamu, K., Masaki, I., and Shingo, M. (2013). "Effects of UV-B irradiation on the levels of anthocyanin, rutin and radical scavenging activity of buckwheat sprouts," *Food Chem*. 141(1), article 32. DOI: 10.1016/j.foodchem.2013.03.032

Yoshida, H., Shimada, K., Hikosaka, S., and Goto, E. (2022). "Effect of UV-B irradiation on bioactive compounds of red perilla (*Perilla frutescens* (L.) Britton) cultivated in a plant factory with artificial light." *Horticulturae* 8(8), article 8080725. DOI: 10.3390/horticulturae8080725

Zagoskina, N. V., Zubova, M. Y., Nechaeva, T. L., Kazantseva, V. V., Goncharuk, E. A., Katanskaya, V. M., Baranova, E. N., and Aksenova, M. A. (2023). "Polyphenols in Plants: Structure, biosynthesis, abiotic stress regulation, and practical applications (review)," *International Journal of Molecular Sciences* 24(18), article 13874. DOI: 10.3390/ijms241813874

Zhang, J., Morris-Natschke, S., Ma, D., Shang, X., Yang, C., Liu, Y., and Lee, K. (2021a). "Biologically active indolizidine alkaloids," *Medicinal Research Reviews* 41(2), 928-960. DOI: 10.1002/med.21747

Zhang, L., Zhu, W., Zhang, Y., Yang, B., Fu, Z., Li, X., and Tian, J. (2014). "Proteomics analysis of *Mahonia bealei* leaves with induction of alkaloids *via* combinatorial peptide ligand libraries," *Journal of Proteomics* 110, 59-71. DOI: 10.1016/j.jprot.2014.07.036

Zhang, Q. W., Lin, L., Fang, F., Cui, B. M., Zhu, C., Luo, S. K., and Yin, R. H. (2023). "Dissecting the functions of COP1 in the UVR8 pathway with a COP1 variant in *Arabidopsis*," *Plant J*, 113(3), 478-492. DOI: 10.1111/tpj.16059

Zhang, S. C., Zhang, L., Zou, H. Y., Qiu, L., Zheng, Y. W., Yang, D. F., and Wang, Y. P. (2021b). "Effects of light on secondary metabolite biosynthesis in medicinal plants," *Frontiers in Plant Science*, 12. DOI: 10.3389/fpls.2021.781236

Zhang, X.-R., Chen, Y.-H., Guo, Q.-S., Wang, W.-M., Liu, L., Fan, J., Cao, L.-P., and Li, C. (2017). "Short-term UV-B radiation effects on morphology, physiological traits and accumulation of bioactive compounds in *Prunella vulgaris* L," *Journal of Plant Interactions* 12(1), 348-354. DOI: 10.1080/17429145.2017.1365179

Zhang, X., Ding, X. L., Ji, Y. X., Wang, S. C., Chen, Y. Y., Luo, J., Shen, Y. B., and Peng, L. (2018). "Measurement of metabolite variations and analysis of related gene expression in Chinese liquorice (*Glycyrrhiza uralensis*) plants under UV-B irradiation," *Scientific Reports* 8, article 6144. DOI: 10.1038/s41598-018-24284-4

Zhaogao, L., Yaxuan, W., Mengwei, X., Haiyu, L., Lin, L., and Delin, X. (2023). "Molecular mechanism overview of metabolite biosynthesis in medicinal plants," *Plant Physiol Biochem* 204, 108125. DOI: 10.1016/j.plaphy.2023.108125

Zhao, Y., Liu, G. Z., Yang, F., Liang, Y. L., Gao, Q. Q., Xiang, C. F., Li, X., Yang, R., Zhang, G. H., Jiang, H. F., Yu, L., and Yang, S. C. (2023). "Multilayered regulation of secondary metabolism in medicinal plants," *Mol. Hortic*. 3(1). DOI: 10.1186/s43897-023-00059-y

Zhong, Z., Liu, S., Zhu, W., Ou, Y., Yamaguchi, H., Hitachi, K., Tsuchida, K., Tian, J., and Komatsu, S. (2019). "Phosphoproteomics reveals the biosynthesis of secondary metabolites in *Catharanthus roseus* under ultraviolet-B radiation," *Journal of*

Proteome Research 18(9), 3328-3341. DOI: 10.1021/acs.jproteome.9b00267

Zhu, W., Yang, B., Komatsu, S., Lu, X., Li, X., and Tian, J. (2015). "Binary stress induces an increase in indole alkaloid biosynthesis in *Catharanthus roseus*," *Frontiers in Plant Science* 6, article 582. DOI: 10.3389/fpls.2015.00582

Article submitted: November 21, 2024; Peer review completed: January 3, 2025; Revised version received: January 12, 2025; Accepted: January 13, 2025; Published: February 5, 2025.
DOI: 10.15376/biores.20.2.Wang