Review article

Environmental factors can impact the secondary metabolites in plants under climate change: a focus on UV-B stress

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Abstract

Different environmental stressors, including ultraviolet (UV) stress, can lead to significant changes in gene expression, metabolism, secondary metabolites, plant height, growth and development, as well as overall plant yield. UV radiation, which ranges from 100 nm to 400 nm, does not participate in photosynthesis and is divided into three categories: UV-A (315–400 nm), UV-B (280–315 nm), and UV-C (100–280 nm). Among these, UV-A is the least harmful to living organisms due to its lower energy and capability to penetrate the ozone layer. In contrast, UV-C is highly damaging but is fortunately absorbed by the atmosphere. UV-B, however, can be harmful to all forms of life at high concentrations. To combat UV stress, plants employ various defense strategies, including thickening their leaves, boosting flavonoid production, and regulating antioxidant levels. UV-B stress also alters the fatty acid profiles in oilseed plants, increasing the levels of palmitic and oleic acids. Exposure to intense UV-B can result in abnormal growth patterns and significant reductions in plant yield. The harmful impacts of UV-B exposure include the suppression of photosystem II (PSII), disruption of electron transport mechanisms, decreased photosynthesis rates, and damage to nucleic acids, membrane lipids, proteins, and photosynthetic pigments. These adverse effects culminate in reduced biomass accumulation, altered nutrient allocation, hindered cell development, and ultimately diminished crop yields.

Keywords: climate change, flavonoid, secondary metabolites, UV stress

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Introduction

The increasing occurrence and severity of extreme weather events worldwide, such as droughts, floods, heatwaves, and wildfires, are increasingly linked to human-caused climate change. Additionally, the depletion of the ozone layer permits higher levels of ultraviolet radiation to enter the Earth's atmosphere (Berglez and Al-Saqaf, 2021). This environmental stress, especially from UV-B radiation, triggers a series of responses in plants that modify gene expression and cellular metabolism. Such changes can result in membrane damage and hinder photosynthesis, ultimately affecting growth and reducing crop yields.

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For thousands of years, medicinal plants have played a crucial role in human healthcare, serving as an essential resource for populations around the globe (Latef, 2023; Rabiei et al., 2019). Today, they continue to be the primary source of healthcare for about two-thirds of the world's population, largely due to their rich content of bioactive phytochemicals (Rabiei et al., 2018). These plants produce a wide variety of secondary metabolites, including tannins, terpenoids, alkaloids, flavonoids, polyphenols, and glycosides (Ghasemi et al., 2019; Ghasemi et al., 2023). These compounds have notable therapeutic properties and provide effective treatments for various health conditions. Moreover, medicinal plants are a significant source of inspiration for modern pharmaceuticals, with many pharmaceutical agents being directly derived from or modeled after the bioactive compounds found in these plants, highlighting their lasting significance (Süntar, 2020). The physiological characteristics and chemical compositions of medicinal plants are influenced by a complex interplay of factors, including environmental conditions and genetic traits. Over time, exposure to different environmental pressures can lead to changes in the genotypes of various plant species, including those used for medicinal purposes, resulting in morphological adaptations and long-term evolutionary consequences (Avasiloaiei et al., 2023). A crucial element that underpins the medicinal properties of plants is their ability to produce secondary metabolites, which are essential for helping plants endure environmental stress. Plants often face challenging conditions that hinder their growth and productivity, which can be classified into biotic and abiotic stresses. Biotic stresses stem from living organisms like viruses, bacteria, fungi, and parasitic plants while abiotic stresses arise from non-living environmental factors such as extreme temperatures, wind, humidity changes, salinity, drought, and flooding. The plant genome is central to regulating the production of these biologically active compounds, thereby influencing growth patterns, developmental processes, and resilience in adverse conditions (Sadashivaiah et al., 2023). When experiencing stress, plants undergo various morphological, physiological, and biochemical changes aimed at alleviating stress effects and minimizing damage or aiding the recovery of affected systems (Khan et al., 2015). A key mechanism through which plants respond to stress involves alterations in plasma membrane receptors. These receptors initiate a series of signaling events that lead to the production of secondary metabolites (SM), enhancing the plant's defensive and adaptive abilities (Atanasov et al., 2015). Therefore, this research aims to explore how environmental factors, particularly UV-B stress, can influence the production of secondary metabolites in plants under climate change.

Gene expression changes in medicinal plants under environmental stress

The formation of secondary metabolites in plant cells is a complex process influenced by environmental signals and the plant's inherent growth traits. A notable example of a key pathway in this process is the shikimate pathway, which is crucial for producing aromatic amino acids such as phenylalanine, tryptophan, and tyrosine. These amino acids act as essential precursors for a wide range of secondary metabolites (Huang et al., 2022). Three main factors significantly affect the production of these metabolites: epigenetic changes, transcriptional regulation, and RNA interference (RNAi) (Al Aboud, 2024). Together, these regulatory mechanisms determine the biosynthesis of secondary metabolites in plants. Regulatory elements can function as either activators or inhibitors of the transcription of genes involved in secondary metabolite (SM) production while RNAi modulates these processes by binding to specific DNA sequences in the promoter regions of target genes (Memelink et al., 2001). As a result, the expression levels of these genes can be influenced by epigenetic markers, affecting secondary metabolite synthesis. Additionally, RNA interference operates post-transcriptionally, managing the production of secondary metabolites through mechanisms similar to small interfering RNA (siRNA). This process involves either degrading messenger RNAs from genes that code for secondary metabolites or inhibiting their translation (Jin et al., 2019). Physiological studies have shown that in comparison to cadmium (Cd) stress alone, zinc oxide quantum dots (ZnO QDs) enhance biomass, decrease Cd accumulation, and increase levels of photosynthetic pigments like chlorophyll and carotenoids. They also boost concentrations of essential nutrients (such as calcium, manganese, and copper) during Cd stress. Importantly, ZnO QDs reduce the levels of reactive oxygen species (ROS), including hydrogen peroxide (H_2O_2) and superoxide (O_2^-) while lowering malondialdehyde (MDA) levels and enhancing the activity of antioxidant enzymes like superoxide dismutase, peroxidase, ascorbate peroxidase, and glutathione peroxidase. Furthermore, ZnO QDs promote the biosynthesis of both primary and secondary metabolites, including total proteins, soluble sugars, terpenoids, and phenolic compounds, thereby alleviating Cd stress in *Salvia miltiorrhiza*. At the molecular level, ZnO QDs stimulate the expression of genes involved in stress signaling, activating downstream target genes related to metal transport, cell wall synthesis, and regulation of secondary metabolite synthesis through transcription factors. This mechanism contributes to improved Cd tolerance in *S. miltiorrhiza*. In summary, these findings clarify how ZnO nanoparticles help mitigate Cd stress, presenting a promising nanomaterial-based approach for enhancing Cd tolerance in medicinal plants (Chai et al., 2024). Furthermore, the increased production of secondary metabolites, particularly those with antioxidant properties, enhances the medicinal and nutritional value of these plants. Advanced biotechnologies, such as CRISPR-Cas9, can be utilized to modify several genes to boost the synthesis of antioxidants like carotenoids, flavonoids, and phenolics in agricultural crops. Metabolic engineering, which allows for the overexpression of key enzymes in these pathways, can also significantly enhance the production of desirable metabolites (Salehi et al., 2020). For example, research indicates that glycyrrhizin levels in licorice stolons rise mainly under severe drought stress, with controlled drought conditions improving the expression of critical genes involved in triterpenoid saponin biosynthesis, thereby directly enhancing glycyrrhizin production (Selmar and Kleinwächter, 2013). Ultimately, identifying the genes and pathways related to stress resistance offers valuable targets for biotechnological applications and genetic modification, providing effective tools to address environmental stresses and improve plant resilience.

What is the ultraviolet stress?

Beyond the Earth's atmosphere, the solar spectrum includes a wide range of wavelengths, but much of this radiation is absorbed before it reaches the surface. Only visible light, along with certain portions of ultraviolet (UV) and infrared (IR) radiation, can penetrate the atmosphere. The potential for damage from radiation increases as the wavelength decreases; however, radiation, as a form of energy, is typically not detectable by the human eye. The electromagnetic spectrum extends from radio waves to gamma rays, with ultraviolet radiation falling between the violet end of visible light and the X-ray range. Although UV radiation is invisible to humans, it can cause fluorescence in some materials, making them emit lower-energy electromagnetic radiation, such as visible light. Notably, many insects can detect UV radiation with wavelengths ranging from 100 to 400 nm (Punch and Wilkinson, 1927). Plants depend on sunlight for photosynthesis, utilizing wavelengths from 400 to 700 nm. UV radiation spans from 100 nm to 400 nm and is divided into three bands: UV-A, UV-B, and UV-C. UV-A (315–400 nm) is the least harmful to living organisms due to its lower energy and ability to pass through the ozone layer with relative ease. While UV-C (100–280 nm) is highly harmful, it is primarily absorbed by the atmosphere. UV-B (280–315 nm), however, is particularly concerning as it can harm all living organisms at elevated levels (WHO, 1994). The ozone layer's integrity is affected by various factors, including volcanic eruptions, climate change, and greenhouse gas emissions. The chemical properties of certain substances determine their effect on the ozone layer. Compounds such as chlorofluorocarbons (CFCs), hydrochlorofluorocarbons (HCFCs), hydrobromofluorocarbons (HBFCs), halons, methyl chloroform, and carbon tetrachloride - historically used as aerosols, refrigerants, fire extinguishers, pesticides, propellants, and solvents - significantly contribute to ozone depletion. Studies suggest that UV-B levels may rise by about 1.3% per decade after 2050

(Eleftheratos et al., 2020). The ongoing depletion of the ozone layer poses a serious risk by allowing greater UV-B radiation to reach the Earth's surface, adversely affecting living organisms. With anticipated increases in UV-B levels, there is an urgent need for continuous monitoring of UV radiation and coordinated efforts to address the factors that contribute to ozone layer depletion, particularly harmful chemical emissions. Increased UV-B radiation could lead to significant ecological impacts, disrupting plant photosynthesis, harming ecosystem health, and posing health risks to both humans and animals. This information highlights the crucial relationship between solar radiation, the ozone layer, and the health of life on Earth, emphasizing the need for sustained environmental protection initiatives.

Gene interference to mediate UV injuries

UV-B sensitive plants accumulate UV-absorbing substances in their outer tissue layers, providing a protective barrier against the harmful effects of UV-B radiation. Key enzymes responsible for synthesizing these protective compounds are specifically induced upon UV-B exposure. For example, *Salvia verticillata* exhibits increased production of phenylpropanoids, including flavonoids, in response to UV-B due to changes in gene expression (Rizi et al., 2021).

During UV-B stress, the redox status within plant cells significantly influences UV-B-induced signal transduction pathways. Formation of reactive oxygen species (ROS) occurs through both non-specific and specific pathways. In non-specific ROS formation, aromatic amino acids and phenolic compounds facilitate energy transfer to adjacent oxygen molecules. This process, along with ROS accumulation, DNA damage, and the biosynthesis of hormones such as salicylic acid, ethylene, and jasmonic acid, mediates non-specific signaling responses (Demkura et al., 2010). In contrast, specific UV-B signaling relies on dedicated receptors, primarily UV RESISTANCE LOCUS8 (UVR8), and involves oxidative stress mechanisms (Cloix and Jenkins, 2008). UVR8 is associated with gene expression activated by low levels of UV-B radiation (Jenkins, 2009) and regulates transcription factors such as ELONGATED HYPOCOTYL5 (HY5) and HY5 HOMOLOG (HYH). Notably, UVR8 controls the expression of over 70 genes upregulated under UV-B radiation, making it a crucial regulator of defense mechanisms essential for terrestrial plant survival under ambient UV radiation (Jenkins, 2009). Another significant signaling pathway involves CONSTITUTIVELY PHOTOMORPHOGENIC1 (COP1), which represses the expression of photomorphogenic genes COP1 functions as an E3 ubiquitin ligase, degrading HY5 and other positive regulators of photomorphogenesis (Prado et al., 2011). Specific genes influenced by varying fluence rates include *PR-1* and *PDF1.2* at high fluence, *PR-5* at intermediate fluence, and *PYROA*, *CHS*, *UBQ3*, *LHCB6*, and *F5D21.10* at low fluence while *MEB5.2* is affected at very low fluence. Research indicates that low-level UV-B exposure promotes the expression of genes involved in plant defense and the production of phenolic and flavonoid (Kumari et al., 2009). The accumulation of UV-absorbing substances is a vital defense strategy for UV-B sensitive plants, underscoring the importance of phenolic and flavonoid compounds in plant protection. Plant responses to UV-B stress involve intricate signaling pathways, both non-specific and specific, crucial for adaptive responses and involving multiple genes and regulatory mechanisms. Understanding these molecular mechanisms offers insights into how plants adapt to environmental stressors, potentially informing agricultural practices aimed at enhancing plant resilience to UV-B radiation. Overall, this research highlights the sophisticated ways plants have evolved to mitigate the harmful effects of UV-B radiation through biochemical pathways and gene regulation, ensuring their survival in changing environments.

Response of secondary metabolites to UV stress

Initially dismissed as mere by-products of primary metabolism, secondary metabolites are now recognized as products of an independent pathway closely linked to primary metabolism. Their production is often enhanced under environmental stress, reflecting their critical role in plant defense mechanisms. UV-B radiation, for example, activates a signaling cascade in plants via UV RESISTANCE LOCUS8 (UVR8), a photoreceptor essential for the synthesis of various secondary metabolites. Upon activation, UVR8 localizes to the nucleus and triggers UV-B responsive genes associated with metabolite production. These secondary metabolites confer both active and passive resistance to plants. Passive resistance is inherent and constitutive while active resistance is induced by metabolites newly synthesized or upregulated under specific environmental conditions (Takshak and Agrawal, 2019). Different plants exhibit variable responses to UV-B exposure, with some demonstrating tolerance and others showing sensitivity. To cope with these challenges, plants employ diverse defense mechanisms, including increased leaf thickness, enhanced flavonoid synthesis, stimulated antioxidant production, and activation of reactive oxygen species (ROS) to neutralize free radicals (Rai and Agrawal, 2017). In *Clematis terniflora*, UV-B exposure significantly increases the production of the indole alkaloid 6-hydroxyl-1H-indol-3-yl (Gao et al., 2016). Early exposure to UV-B increases vindoline and catharanthine levels, but prolonged exposure reduces these while increasing vinblastine content up to day 15 (Liu Ying et al., 2011). *Coleus forskohlii* also shows a notable increase in total alkaloid content in leaves and roots under UV-B stress (Takshak and Agrawal, 2019). Jaiswal and Agrawal (2021)reported enhanced monoterpene levels in two *Curcuma* species (*C. caesia* and *C. longa*), with sesquiterpenes specifically increasing in *C. longa*. This elevated terpene content contributes to higher essential oil content in both species. Loreto and Schnitzler (2010)highlighted isoprene induction under UV-B stress in European oak trees. Flavonols, flavones, and anthocyanins act as ROS scavengers, providing protection under UV-B exposure. Kumari et al. (2009) reported a significant increase in total phenolic compounds in *Acorus calamus* subjected to UV-B treatment. *Coleus forskohlii* also shows enhanced anthocyanin levels in leaves and roots under UV-B stress. The importance of UV-B for phenolic production, especially anthocyanins, is evidenced by exclusion experiments showing reduced anthocyanin content in red-leafed lettuce plants (Chalker-Scott, 1999). Müller et al. (2013)observed flavonoid induction in *Arabidopsis* under high light and UV radiation. Similarly, Kumari and Agrawal (2010)recorded increased flavonoid production in *Cymbopogon citratus* under heightened UV-B exposure. Lipid profiling of *Olea europaea* reveals increased palmitic and oleic acid levels under high UV-B doses, with the ratio of unsaturated to saturated fatty acids remaining unchanged (Dias et al., 2018). In *Spirulina platensis*, UV-B exposure reduces saturated fatty acids while increasing unsaturated fatty acids (Gupta et al., 2008). In *Glycine max* (cultivars JS-335 and PS-1042), total oil content decreases in response to enhanced UV-B radiation. Fatty acid profiling indicates that saturated fatty acids, including stearic and palmitic acids in JS-335 and only palmitic acid in PS-1042, are reduced while total unsaturated fatty acids increase under UV-B conditions. Among monounsaturated fatty acids (MUFA), oleic acid levels decrease in both cultivars, whereas polyunsaturated fatty acids, such as linoleic and linolenic acids, increase in JS-335, with only linolenic acid being enhanced in PS-1042 (Choudhary and Agrawal, 2015). Secondary metabolites play a vital role in plant adaptation to stress, particularly UV-B radiation, demonstrating the complexity of plant metabolic pathways. Different plants exhibit distinct mechanisms and capabilities to respond to UV-B stress, leading to varied outcomes in metabolite production. Understanding these responses can inform agricultural practices and help develop crops more resilient to environmental stresses (Table 1). Overall, this research highlights the intricate relationship between environmental stressors and plant metabolic responses, emphasizing the evolutionary significance of secondary metabolites in plant survival.

Metabolism and physiology of plants

Anthropogenic activities, particularly the increase in chlorofluorocarbons (CFCs), have led to a reduction in stratospheric ozone levels, resulting in higher levels of ultraviolet-B (UV-B) radiation reaching the Earth's surface (Kumar et al., 2016). In plants, UVR8 photoreceptors play a critical role in detecting UV-B radiation (Podolec et al., 2021). Even low doses of biologically active UV-B wavelengths can trigger signaling pathways, modify hormone profiles, influence gene expression, affect metabolite accumulation, and change various aspects of plant morphology,

Table 1
Effect of UV and some environmental stresses on plant metabolites

Plant Specie	Metabolite name	Environment Factor	Change (+, -)	Reference
Asparagus officinalis	Flavonol quercetin-4′-O-monoglucoside	UV-B	+	Eichholz, et al., 2012
Nasturtium officinale	Glucosinolate	UV-B	+	Reifenrath and Müller, 2007
Withania somnifera	Phytosterols	UV-B	+	Takshak, and Agrawal, 2014
Mahonia bodinieri	Alkaloids	30 and 50% Full sunlight	+	Li, et al., 2018
Withania somnifera	Anthocyanins, lignin, tannins	UV-B	+	Takshak, and Agrawal, 2014
Chrysanthem	Phenolic acids	UV-B	+	Ma., et al., 2016
Scutellaria baicalensis	Baicalin	Drought	+	Cheng, et al., 2018
Labisia pumila	Anthocyanins	Drought	+	Jaafar, et al., 2012
Artemisia	Artemisinin	Drought	+	Verma, and Shukla, 2015
Hypericum brasiliense	Total phenolics	Drought	+	de Abreu, and Mazzafera, 2005
Oilseed rape	Oil content	Drought	-	Ghassemi-Golezani et al., 2023
Safflower	Oil content	Drought	-	Farzi Aminabad et al., 2021

physiology, and growth (Mannucci et al., 2020; Nocchi et al., 2020; Yadav et al., 2020; Zhao et al., 2020). However, exposure to high-intensity UV-B radiation can induce stress, resulting in abnormal growth patterns and substantial yield losses. The harmful effects of UV-B exposure include the suppression of photosystem II (PSII), disruption of electron transport chains, decreased photosynthetic efficiency, and damage to nucleic acids, membrane lipids, proteins, and photosynthetic pigments. As a result, this stress can lead to reduced biomass accumulation, altered nutrient distribution, and impaired cellular development (Mmbando et al., 2020; Rizi et al., 2021). These findings highlight the considerable risks that increased UV-B radiation poses to plant systems as a consequence of human-induced atmospheric changes. With rising UV-B exposure, agricultural productivity and ecosystem health may face serious challenges. This underscores the importance of further research aimed at developing strategies to mitigate UV-B stress and enhance plant resilience, which is essential for ensuring sustainable agricultural practices and preserving terrestrial ecosystems amid environmental changes (Fig. I).

Growth and development

Modifications in cell division and expansion can significantly influence plant structure and height, often leading to a reduction in leaf area while increasing leaf thickness. These adjustments are associated with changes in stomatal and trichome densities. Ultrastructural and anatomical research indicates that UV-B radiation causes alterations in these densities (Rai and Agrawal, 2020), as well as changes in the structure of epidermal cells, palisade tissue, and spongy mesophyll (Hamid et al., 2019). Generally, the growth of UV-B-sensitive plants, including their height and leaf area, tends to decrease, with the extent of reduction varying by plant type and cultivar (Tevini and Teramura, 1989). Additionally, UV-B irradiation has been associated with swelling in the endoplasmic reticulum and thylakoid membranes (Bornman and Teramura, 1993). Changes in CO_2 assimilation rates can significantly impact overall productivity and yield. Increased UV-B radiation affects both the oxidizing and reducing components of

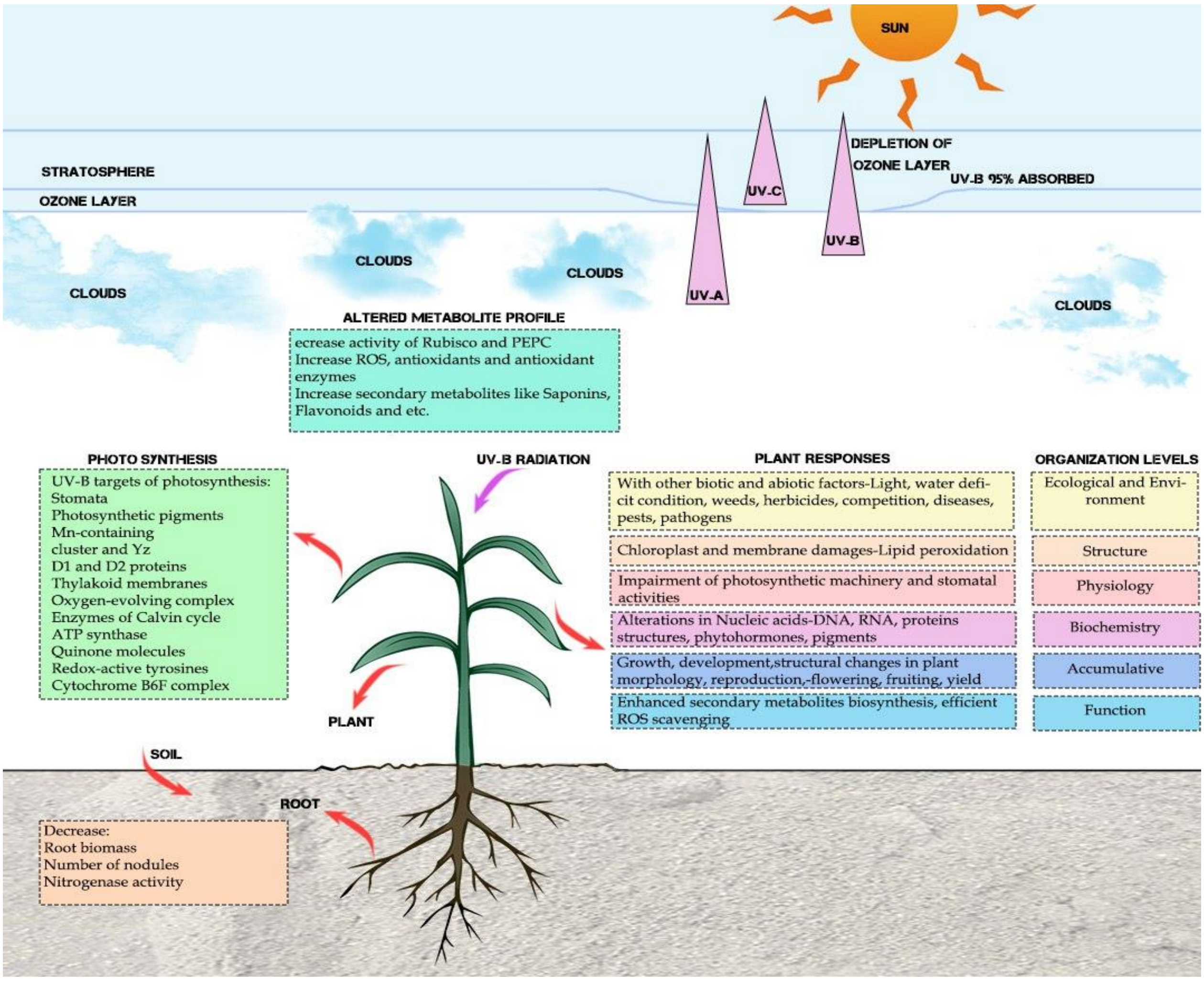

Fig. I. Plant response to UV-B radiation

photosystem II (PSII). Specifically, the oxidizing side, which includes the water-splitting complex (WSC) or oxygen-evolving complex (OEC) and P680, can be compromised by UV-B exposure, disrupting the functional relationship between these components (Hideg and Vass, 1996). Elevated UV-B levels lead to reductions in biomass, total dry matter production, and marketable yield. A multitude of studies worldwide have explored the effects of increased UV-B radiation on plant development (Zlatev et al., 2012). Critical growth parameters, including plant height, leaf volume, and flowering patterns, are influenced by UV-B exposure (Caldwell et al., 2007). Furthermore, UV-B radiation affects reproductive processes in numerous ways. Seed germination and early seedling development are particularly vulnerable to UV-B, with this sensitivity being linked to the developmental stage and the adaptive responses that plants develop to manage increased UV-B levels. Llorens et al. (2015)noted that key stages in flowering and pollination, such as anther dehiscence, pollen tube germination, and stigma penetration, are particularly susceptible to UV-B stress. They also observed that UV-B radiation tends to delay the onset of flowering in annual plants, likely due to the stress induced by UV exposure. Moreover, interactions with pollinators, such as bees, diminish under elevated UV-B conditions. The increased UV exposure can result in smaller flower sizes, reduced pollen viability, and overall declines in reproductive success, affecting fruit and seed set across various species (Llorens et al., 2015). Overall, heightened UV-B radiation poses considerable challenges to plant development by affecting not only growth parameters like height and leaf size but also compromising reproductive success and overall productivity. The varying sensitivity of different developmental stages to UV-B stress highlights the urgent need for further investigation into the adaptive mechanisms employed by plants. Understanding these impacts is essential for formulating strategies to mitigate the effects of increased UV-B exposure, particularly in light of changing environmental conditions that could ultimately threaten food security and ecosystem sustainability.

Conclusion and future prospects

Increasing atmospheric concentrations of pollutants, including carbon dioxide and chlorofluorocarbons, are responsible for damaging the ozone layer, which in turn allows more ultraviolet (UV) radiation to reach the Earth's surface. This increase in UV radiation can lead to notable changes in plant growth and development. For example, UV exposure commonly results in thicker leaf structures, alterations in plasma membrane composition, and heightened activity of antioxidant enzymes. Essential biological macromolecules, such as proteins and nucleic acids, are particularly susceptible to the damaging effects of UV-B radiation, as they effectively absorb this portion of solar radiation. Consequently, any increase in UV-B radiation poses a significant threat to living organisms. To combat this, UV-B sensitive plants have developed strategies to accumulate UV-absorbing compounds, emphasizing the role of phenolic and flavonoid compounds in plant defense mechanisms. The plant response to UV-B stress involves complex signaling pathways, incorporating both non-specific and specific responses that are essential for adapting to environmental stressors. These pathways engage multiple genes and regulatory mechanisms, highlighting a sophisticated level of molecular response to UV stress. Understanding these molecular processes offers valuable insights into how plants cope with increased UV exposure, which could help improve agricultural practices aimed at enhancing plant resilience. As UV-B exposure continues to rise, the potential consequences for agricultural productivity and ecosystem health become increasingly concerning. This scenario underscores the urgent need for further research focused on developing strategies to mitigate UV-B stress and bolster plant resilience. Such efforts are crucial for ensuring sustainable agricultural practices and preserving terrestrial ecosystems in light of ongoing environmental changes.

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