REVIEW



Ultraviolet-B radiation in relation to agriculture in the context of climate change: a review

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Abstract

Over the past few decades, the amount of ultraviolet-B radiation (UV-B) reaching the earth's surface has been altered due to climate change and stratospheric ozone dynamics. This narrow but highly biologically active spectrum of light (280–320 nm) can affect plant growth and development. Depletion of ozone and climate change are interlinked in a very complicated manner, i.e., significantly contributing to each other. The interaction of climate change, ozone depletion, and changes in UV-B radiation negatively affects the growth, development, and yield of plants. Furthermore, this interaction will become more complex in the coming years. The ozone layer reduction is paving a path for UV-B radiation to impact the surface of the earth and interfere with the plant's normal life by negatively affecting the plant's morphology and physiology. The nature and degree of the future response of the agricultural ecosystem to the decreasing or increasing UV-B radiation in the background of climate change and ozone dynamics are still unclear. In this regard, this review aims to elucidate the effects of enhanced UV-B radiation reaching the earth's surface due to the depletion of the ozone layer on plants' physiology and the performance of major cereals.

Keywords Ultraviolet-B radiations · Cereals · Climate change · Stratospheric ozone · Greenhouse gases

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Introduction

Presently, the world's major problem is feeding the masses with limited resources. Reducing the yield gap is a key approach in the crop production system to provide adequate food for 9 billion people worldwide by 2050 (Novotny et al. 2023). The world population is continuously increasing, while global climate change degrades our ability to increase food production on a global scale (Godfray et al. 2010). Global food security greatly depends on cereal production, which yearly accounts for almost 26 million tonnes, which clearly indicates the importance of cereals and cereal products (FAO 2022). Cereals and their products are the principal component in most human foods (McKevith 2004; Ahmad et al. 2023), both in developing and developed countries, offering a huge amount of nutrients and dietary energy. Cereals are comprised of almost 75% carbohydrates and 6–15% protein and thus, supply more than 50% of energy globally (Laskowski et al. 2019). The staple cereals are the basis for global food security and with the estimated rise in population, the demand for cereals will also increase to fulfil the caloric needs of the globe (Godfray et al. 2010). The ozone sheet in the stratosphere reduces the amount of incoming ultraviolet B radiation (UV-B) reaching the earth's surface (Bernhard et al. 2020; Dawood et al. 2022). However, its depletion is leading to a rise in the amount of solar radiation, particularly UV-B, which is undoubtedly harmful to life on earth (Bernhard et al. 2020). One of the major causes of ozone depletion is the anthropogenic release of compounds containing bromine and chlorine into the environment (Hossain 2023). Chlorofluorocarbon (CFC) has the highest potential to diminish the ozone layer; refrigerators, burning tyres, and automobile exhausts are the primary sources of this gas in the open environment (Zhang et al. 2023).

The reduction in the stratospheric ozone because of climate change over the last several years has diverted the attention of agricultural scientists towards its effects on plants. The ozone dynamics over the southern hemisphere are shown in Fig. 1. It is a serious threat to agricultural production. Besides photosynthetically active radiations (PAR) with a detectable range of 400–700 nm, plants are also subjected to ultraviolet radiations, i.e., UV-A, UV-B, and UV-C with 320–390 nm, 280–320 nm, and below 280 nm wavelength, respectively. The relative percentages of the PAR and UV portions of the incoming solar energy under natural conditions with a clear sky range from 42.7 to 71% and 2.8 to 7%, respectively (Escobedo et al. 2011). While UV has a further subdivision, i.e., UV-A has a 95%, and UV-B has a 5% share. UV-A radiation is not very harmful to plants (Nawkar et al. 2013). However, UV-B radiation has detrimental effects on the growth and development of plants because it induces certain morphological and physiological changes in plants (Robson et al. 2015). The detrimental impacts of UV-B radiation on DNA are evident, indicating that it affects all living organisms' normal living processes (Rastogi et al. 2010), including plants. Higher UV-B levels can damage living cells (Nawkar et al. 2013). The changes monitored in the ozone layer in the past decades have affected the amount of UV-B impacting the earth's surface, with subsequent influence on human health, biogeochemical cycles, terrestrial, and marine ecosystems (Bais et al. 2015).

The future level of surface UV-B radiation and the prospective effects of global climate change on UV levels are still unknown (Andrady et al. 2012). Despite the commencement of the ozone recovery, no considerable decrease in UV-B radiation has been detected (Bais et al. 2015). Many locations are subjected to elevated levels of incoming UV-B radiation regardless of the efforts to minimize CFC emission. Studies have been carried out to investigate the influence of UV-B radiation on plants, mostly in controlled (greenhouse or growth chamber) conditions (Caldwell et al. 2007). Determining the impact of increased UV-B radiation under field conditions is vital to evaluating the influence of this stress factor on the performance of plants (Parisi et al. 2003;



Fig. 1 Extension of the ozone hole over the southern hemisphere (from 1979–2019). The red and yellow color denotes higher ozone columns, while blue denotes lower ozone columns (https://www.eea.europa.eu/data-and-maps/figures/maximum-ozone-hole-area-in-7)

Abreu et al. 2023). The harmful effects of UV-B radiation on plant performance are widely reported, but the effect of an increased level of UV-B on the productivity of grain crops is under debate (Hidema and Kumagai 2006). It is imperative to fully recognize how the plants will react to the increase or decrease in UV radiation under open conditions within the framework of climate change (Barnes et al. 2019, 2022a, b). Furthermore, it is challenging to evaluate the response of plants to changing UV-B radiation simultaneously with other multiple environmental stresses produced due to climate change, but it is of utmost importance in the perspective of the future environment (Virjamo et al. 2014). The direct and indirect impacts of climate change-related phenomena are likely to affect the future level of UV radiation and could modify the impacts of the projected ozone recovery on UV radiation (Bais et al. 2015). The purpose of this study is to review the UV-B radiation against the background of climate change and its subsequent effects on crops.

Lockdown due to the coronavirus pandemic and ozone layer

CO₂ emissions are one of the most significant causes of global warming, and a rise in CO₂ subsequently reduces the ozone layer. Most countries imposed lockdowns due to the COVID-19 pandemic, which ranged from several weeks to months, and significantly aided in the reduction of CO₂ emissions from transportation and other sectors in the short term (Table 1). Furthermore, between February and June 2020, global emissions of ozone-depleting substances like nitrogen oxides (NOx) decreased by almost 15% as a result of the lockdown (Miyazaki et al. 2021). Other main pollutant gases like CO, SO_2 , O^3 , and volatile organic compounds (VOCs) have been studied in various countries during the lockdown. Considerable variations in their amounts before and during the lockdown were observed. A reduction of 21-26%, 16-26%, and 37-57% in the concentrations of CO, SO₂ and volatile compounds, respectively, were recorded in China during the lockdown (Li et al. 2020).

On the other side, an increase in ozone (O_3) of 20.5% was also noticed during the same period (Li et al. 2020).

Table 1Reduction in CO_2 emission due to coronavirus lockdown(NASA 2020a)

Country	Reduction in CO ₂ %
United States of America	7.5
United Kingdom	48
China	18
Italy	27
Pakistan	17

Similar results were reported in another Italian study, where lockdown was associated with decreases in SO₂, CO, and benzene levels of 20-27%, 5-75%, and 48-68%, respectively. However, the concentration of ozone significantly increased, rising by almost 50% (Collivignarelli et al. 2020). Nakada and Urban (2020) reported a decrease of 36-65% and 18-33% in the concentrations of CO and SO₂, respectively, with an increase of around 30% in the ozone during the lockdown in Sao Paulo. A study conducted in 22 cities in India reported a reduction of 10% in CO concentration with no change in the concentration of SO₂. Yet, a 17% increase in O³ concentration was observed (Sharma et al. 2020). Chinese cities reported a nearly 40% reduction in greenhouse gas emissions by March 2020 in comparison to the same period in 2019 (Chen et al. 2021; Mina et al. 2021). Similar findings were made in India, Japan, and Europe. According to the European Environment Agency 2020, NO2 emission rates, for instance, decreased by 50% in Europe compared to 2019 and by 20-30% in the United States. Throughout South America in February and March of 2020, levels of particulate matter (PM2.5 and PM10) including SO₂ and CO dropped, and the ozone layer's thickness also declined (Feldman et al. 2020).

Furthermore, fossil fuel consumption across the world declined due to the impact of the lockdown on industries, transportation, and other sectors using fuel. This reduction imposed a positive effect on the earth's environment, like a reduction in GHG emissions and a subsequent increase in the ozone layer's thickness (Chakraborty and Maity 2020). Consequently, this lockdown due to COVID-19 was proven to be effective for the ozone layer and was found to have a healing effect on ozone because when the activities are limited, the ozone destruction is also controlled. Ecosystems have been significantly recovered due to lockdown, but as the lockdowns were for the time being, their consequences might not be observed in the future.

Stratospheric ozone reduction, UV-B radiation, and climate change

The ozone layer is approximately 10–50 km thick (the lower portion of the stratosphere) over the earth; however, its thickness varies from season to season and region to region. Although ozone is present in the entire atmosphere, its greatest concentration can be found 19–30 kms above the surface of the earth. This sheet of ozone-concentrated air is generally called the "ozone layer". The average concentration of ozone is almost 300–350 DU (Dobson Units) (AFEAS 1995). The stratospheric ozone layer is crucial in safeguarding the biosphere from hazardous UV radiation from the sun (Rozanov 2020). This layer makes the stratosphere's temperature skeleton and affects the surface climate directly (Bernhard et al. 2020). It is of the utmost importance to comprehend the previous and future amounts of ozone at various atmospheric levels, as well as its consequences on UV radiation, human health, and agriculture (Rozanov 2020).

The measures taken as a result of the Montreal Protocol and its amendments (MPA) to reduce the emission of GHGs to prevent the lessening of the ozone layer and guarantee its recovery in the future seem to fail in attaining their objectives as the continuing depleting trend in ozone in the lower stratosphere is reported (Ball et al. 2018). One piece of evidence supporting this argument is the emergence of a big ozone hole over the Arctic in the near future, i.e., 2020 (Witze 2020). According to Mohammed and Trapley (2010), the amount of UV-B radiation reaching the earth will not be able to be reduced to pre-industrialization levels by 2050, even if all countries follow the Montreal Protocol. Despite efforts to reduce the use of ozone-depleting substances, mathematical models predict increased UV-B radiation levels in the future, which will be further impacted by climate change interactions (Barnes et al. 2022a, b). NASA (2020b) compared the ozone concentration over the arctic region between March 12, 2020, and March 12, 2019 and reported that the ozone concentration was at its lowest level (205 Dobson units) for 2020, and that such low levels are unusual (Fig. 2).

Smyshlyaev et al. (2020) informed that the scenarios presented by the World Meteorological Organization (WMO) regarding the decline in the emission of "halogen-containing ozone depleting substances" (HODS) into the atmosphere in the last decade, i.e., 2010-2020, are possibly overestimated. According to Pawson et al. (2014), for the period 2008–2013, the stratospheric ozone layer was 6% thinner than for the period 1964–1980, with the highest depletion recorded in the southern latitude zones, and this depletion may become a significant factor in determining the future performance of crops (Wijewardana et al. 2016). The range of UV-B radiation received daily in summer is between 2 and 9 kJ/m² in 40°N and 40°S latitudes, and this level compared to 1994 is higher by almost 3 kJ m⁻² (McKenzie et al. 2007). Moreover, this level is expected to increase further in the twenty-first century (WMO 2007).

Estimates project an increase in the UV-B level, but uncertainty exists between projected climate changes and their interactions with atmospheric chemistry (Taalas et al. 2000). Among GHGs, the more powerful are ozone-depleting substances (ODS) (Hodnebrog 2020), like CFC-11, which is 19000, and CFC-12, which is 23000 times more radioactively efficient (in W m⁻² per part per billion) than CO_2 (Myhre et al. 2013). Likewise, CFC-11 has 7,000 and CFC-12 has 11,000 times more potential for global warming than CO_2 (Fahey 2018). ODS are thus a serious threat



Fig. 2 Ozone concentration over Arctic regions on March 12, 2020 (a) in comparison with March 12, 2019 (b). Dark and light blue color shows low levels, while red and yellow color depicts the higher concentration of ozone (NASA 2020b)

to the ozone layer, and the increase in GHG emissions and ODS due to anthropogenic activities is raising the planet's temperature, reducing the ozone layer, and thus giving more chances for this deleterious radiation to enter the earth's surface. The gases (ODS) are both recognised as potent GHGs and are primarily responsible for the ozone hole over Antarctica. The physical interaction between climate change and ozone depletion is far more complex than previously assumed, and the focus is on understanding this interaction (Tang et al. 2011). Both can work bilaterally, i.e., climate change and ozone dynamics interact in several ways to affect the global ecosystem (Fig. 3).

The observed variations in the UV radiations may be caused by changes in the ozone layer or by changes in other factors such as shifts in surface reflectance, clouds, or aerosols (McKenzie et al. 2011). Ozone recovery is predicted in non-polar regions (UNEP 2006), while in polar regions, a rapid loss of the ozone may occur (Rex et al. 2006); thus, changes in the ozone in the future are predicted depending on the emission of GHGs (Montzka 2010). Climate change alters atmospheric circulation, causing a difference in the ozone on a regional basis, subsequently decreasing UV in some regions and increasing UV in others (Tilmes and Salawitch 2008). Rather than previously predicted zone recovery,

degradation is predicted due to an increase in GHG emissions, accelerating the ozone depletion rate in the coming decades (Dreyfus et al. 2023). A decline of 1% in the ozone layer increases exposure to UV by 2–3% in the lower atmosphere (Reddy et al. 2010).

UV-B radiation and agriculture

The three cereal crops playing a significant role in the world food chain are wheat, maize, and rice. The UV radiations from the sun, particularly UV-B radiation, affect the performance of terrestrial plants, causing damage at the molecular level and producing variations in plant physiology and morphology, thus, reducing yield (Fig. 4). Understanding the response of plants to UV-B radiation is of significant importance in evaluating its effect on terrestrial ecosystems (Bornman et al. 2019). Although UV-B radiation represents a very narrow portion of the solar spectrum, it imposes a crucial photobiological effect on animals and plants because of its absorption by key molecules like lipids, proteins, phytohormones, and nucleic acids (Singh et al. 2012).

Higher UV-B radiation enhances harmful effects on insects health and behaviour and subsequently their interaction with plants via photomorphogenic changes and stimulation of the production of defensive materials (Yin et al.



Fig. 3 Pathways by which climate change and ozone dynamics affect the global ecosystem. Adapted from Barnes et al. (2022a, b)



Fig. 4 UV-B impacts on morphological, physiological, molecular, and yield attributes of plants Kataria et al. (2014). Adapted from

2018; Escobar-Bravo et al. 2017). In general, solar UV radiation is greater in lower latitudes, with the exception of the ozone hole region. As a result, species residing at lower latitudes are more susceptible to its damaging effects (Meador et al. 2009). This causes insects to evolve defensive mechanisms and other adaptations against UV-B radiation in the environment (Gaudreau et al. 2017). Plant-dwelling mites mainly reside on the lower leaf surfaces of their host plants (Sudo and Osakabe 2011). In addition to topographic differences between adaxial and abaxial leaf surfaces (Sudo and Osakabe 2013), the preference for residing on lower leaf surfaces by tiny mites (Kiritani 2013) has been ascribed to the avoidance of harsh environments on upper leaf surfaces such as rain (Rêgo et al. 2013), radiant heat (Lu et al. 2014), and UV-B (Barcelo 1981). Studies have demonstrated significant biological impacts of UV-B radiation on mites residing on plants (Suzuki et al. 2009; Ohtsuka and Osakabe 2009). Genus Tetranychus, which comprises the two-spotted spider mite (T. urticae Koch), is one of the most important spider mites acting as horticultural pests due to their robust fertility, extremely wide host range, and development of acaricide resistance (Van Leeuwen et al. 2015).

Therefore, the use of UV-B for spider mite control has received attention (Short et al. 2018). UV light is also important for various biochemical processes associated with plant defence responses against insect herbivory (Roberts and Paul 2006). Studies revealed that UV-B induced effects on plant secondary chemicals in turn affect plant-insect interactions like decreased herbivory under elevated UV-B light levels (Caputo et al. 2006; Izaguirre et al. 2007). This decrease in insect herbivory under elevated UV-B conditions has been attributed to changes in nutritional quality (Roberts and Paul 2006) or plant secondary chemistry (Izaguirre et al. 2007) as well as resulting from direct effects of UV-B on insect herbivore behavior (Caputo et al. 2006). These consequences of higher UV-B levels have led to reduced insect oviposition rates (Fountain et al. 2023), insect performance (Lindroth et al. 2000), and plant damage (Liu et al. 2023). In soybean, UV-B-induced reductions in herbivore attack have been related to increases in phenolics (Zavala et al. 2001). Similarly, Veteli et al. (2003) observed that insect abundance was higher under elevated UV-B than under shade or UV-A, however, insect damage levels did not differ between control and elevated UV-B treatments.

In contrast to the effects of UV radiation on plant-insect interactions, the impact of enhanced UV light on plant disease (bacteria and fungi) is limited and not well understood (Bidart-Bouzat and Imeh-Nathaniel 2008). Some studies suggested that plant resistance against pathogens may be improved by exposure to UV radiation, as this type of radiation induces plant defence responses (Roberts and Paul 2006). UV light may also directly affect fungal pathogens by suppressing spore production and their ability to infect a host plant (Bidart-Bouzat and Imeh-Nathaniel 2008). Research conducted thus far has shown both an increase and decrease in disease damage in response to elevated UV-B radiation (Priya et al. 2016). Effects of UV-B on diseases and insects could be attributed to direct effects on their growth and indirect effects through changes in tissue characteristics and composition. Studies showed that thrips consumed less leaf tissue, and Lepidopeteran larvae had lower survival in a laboratory assay when fed on leaves grown under near-ambient solar UV-B compared with leaves from UV-B excluded plots (Priya et al. 2016). The lower larval survival was due to higher levels of soluble phenolics and lower lignin content in the foliage subjected to UV-B radiation (Priva et al. 2016).

Ultraviolet-B radiation alters the morphology, and physiology of plants, which can directly influence disease and pest incidence. UV-B can affect carbohydrate, nitrogen, and fiber content in leaves, indirectly affecting the growth and survival of insects. Similarly, secondary metabolites (such as jasmonic acid and phenolics) produced by plants exposed to UV-B can influence insect behaviour and incidence by acting as an attractant or repellent. Insects that are sensitive to ultraviolet radiation shield themselves from its harmful effects by avoiding sections of plants where protective compounds have accumulated and instead feeding on the undersides of leaves, where UV-B penetration is less (Priya et al. 2016).

An increase in UV-B could cause a shift in the relative competitiveness of some plant species, such as weeds and crops. Increased UV-B levels have been shown in studies to affect the competitive balance between crops and weeds, while weed competition can reduce crop yield (Bornman et al. 2019). Li and Wang (2001) noticed that elevated UV-B in a wheat ecosystem caused a reduction in weed quantity and biomass, species population, and soil macroanimals. A change in species diversity was also observed in the same study. Their outcomes disclosed that the competitive balance between weeds and wheat could be altered under elevated UV-B levels. Changes in the balance of competition have been seen in mixtures of plants exposed to increased UV-B radiation, despite the fact that the respective monocultures of these plants exhibited no particular impacts (Bornman et al. 2019).

Changes in species competition relationships will be one of the most significant ecosystem-level effects of stratospheric ozone reduction, particularly in non-agricultural ecosystems (Wu et al. 2019). From the perspective of species competition, even a minor reduction in plant height caused by UV-B radiation may eventually be significant if various species are affected to varying degrees, resulting in a shift in the competent balance between species (Wu et al. 2019). Still, the fundamental mechanisms by which a change in UV-B level affects the competitive relationships between plant species remain poorly understood.

UV-B radiation effects on plant morphology

Plants are sessile and lack the ability to move in pursuit of a suitable environment for optimal growth and development. Their fixed nature compels them to finish their life span in the ecosystem in which they are growing. It is of utmost worth to understand the response of plants to UV radiation under natural conditions in the context of climate change. Wide interspecific and intraspecific variations in plant growth, dry matter production, and physiological and biochemical alterations in response to UV-B irradiation have been observed (Fedina et al. 2010). Some plant species did not show any changes in response to UV-B radiation, and many apparently benefited in their growth; however, the majority of the species, such as rice and maize, are susceptible and suffer harm (Hidema et al. 2007; Lidon 2012; Du et al. 2011). Numerous plant species have been shown to have dwarf plant architecture after being exposed to UV radiation. UV-B exposure typically has detrimental effects on the growth, morphology, and developmental processes of plants (Chaudhary and Agrawal 2015; Dotto and Casati 2017). Enhancement in leaf thickness, leaf curling, and modifications in leaf width and shape are the most often documented UV-B-induced morphological changes (Robson and Aphalo 2012; Klem et al. 2012).

Reduction in leaf area is one of the most constant responses of the plants to UV-B exposure (Wargent et al. 2009, Fierro et al. 2015). This reduction in leaf area is due to a reduction in cell growth and inhibition of cell division, which appears to vary from species to species (Hectors et al. 2010). Likewise, reduction in stem elongation has also been documented in a number of plant species (Hofmann and Campbell 2011; Germ et al. 2013). Roro et al. (2017) exhibited that the decline in leaf area and shoot elongation in pea when subjected to UV-B was related to lower gibberellin levels in young leaves and tissues of the apical stem. Yet, it is unclear whether the reduction in shoot elongation in plants exposed to UV-B is only due to lower cell growth or whether UV-B also affects cell division (Dotto and Casati 2017).

In addition, there is substantial evidence that UV-B radiation promotes axillary branching and/or tillering (Kumari et al. 2023). The aboveground effects are likely to have an impact on the roots: shoot ratio and UV-B radiation have been reported to result in a greater allocation of biomass to the roots (Bussell et al. 2012). The correct timing of flowering is of utmost importance for a successful seed set. UV-B radiation changes the flowering time in many species like maize, *Vigna raidate*, Arabidopsis, and *Phaseolus vulgaris* (Yan et al. 2012; Mark et al. 1996; Tevini 1997; Rajendiran and Ramanujam 2004). Flowering was delayed in all these crops, but the molecular specifics behind this mechanism are not available (Dotto and Casati 2017). UV-B exposure reduces plant inflorescence elongation and increases axillary growth, indicating that UV-B plays a significant role in retarding plant growth (Hectors et al. 2007).

There is also relatively little information about UV-B effects on flower development, and the few studies that have examined its effect on fruit development have mostly described changes in the composition of secondary metabolites (Alonso et al. 2016). These modifications are frequently inferred as a result of plants reallocating resources while growing in the presence of UV-B light. Higher UV-B exposure clearly reduced the relative growth rate and nitrogen productivity as the leaf area ratio, productivity, and leaf nitrogen productivity were all reduced (Eissa et al. 2011). Concisely, plants subjected to a higher level of UV-B radiation show a reduction in both biomass and dry matter production. A summary of the various developmental processes in plants stimulated by UV-B radiation is presented in Table 2.

UV-B radiation influence on plant physiology

Higher levels of UV-B exposure can harm plant cells, which consequently affect the plant's physiological activities as a whole. Dicotyledons are typically more susceptible than monocotyledons when subjected to UV-B radiation (Kataria et al. 2013). UV-B can damage DNA and induce mutations in DNA replication (Schmitz-Hoerner and Weissenböck

 Table 2
 UV-B radiation impacts on various plant developmental processes

Reference
Biever (2014)
Yan et al. (2012)
Tong et al. (2008)
Wijewardana et al. (2016)
Hectors et al. (2010)
Fierro et al. (2015)
Yan et al. (2012)
Dotto and Casati (2017)
Jaiswal et al. (2023)
Xie et al. (2023)

2003). UV-B radiation, as described by Staxén et al. (1993), affects the cytoskeleton of plant cells by creating breakage in cortical microtubules, which can, in turn, inhibit cell division. Additionally, UV-B radiation destroys amino acids, resulting in the inactivation of enzymes and proteins (Grossweiner 1984). In the presence of oxygen, UV-B radiation also damages lipids in plant cell membranes, a process known as lipid peroxidation (Kramer et al. 1991).

The impact of UV-B radiation on plant photosynthesis depends on several factors, including crop species, amount of UV-B, PAR to UV-B ratio, and cultivars (Fernando et al. 2012). UV-B targets several plant tissues and processes, but the photosynthetic apparatus is the one with the greatest susceptibility to UV-B, and it significantly contributes to the overall damage caused by UV-B (Lidon and Ramalho 2011). The impact of UV-B on the photosynthetic apparatus can be seen at different levels, including changes in leaf anatomy, morphology and the destruction of photosynthetic pigments (Jenkins 2009). UV-B decreases the content of photosynthetic pigments in the chloroplast, particularly chlorophyll a, which is the major pigment in photosynthesis (Ayash et al. 2017; Sebastian et al. 2018). The reduction in net photosynthetic rate is much higher than the reduction in stomatal conductance due to enhanced UV-B (Fernando et al. 2012). UV-A radiation stimulates stomatal opening, while UV-B radiation induces its closure (Brestic et al. 2023).

Studies reported the negative effects of UV-B on stomatal conductance, which decreases the amount of CO₂ available for photosynthesis (Cechin et al. 2018; Reyes et al. 2019). UV can damage important cellular components like protein and lipids (Fedina et al. 2010). The chloroplast is the target site for UV-B radiation that significantly impairs photosynthetic functions (Lidon et al. 2012a, b). UV-B has an indirect deleterious effect on chlorophylls a and b in plants (Salama et al. 2011), thus affecting photosynthesis. UV-B radiation has a more deleterious effect on PSII and cytochrome than PSI (Lidon et al. 2012a, b). Carotenoids are less susceptible to an increase in UV-B than chlorophyll (Pfundel et al. 1992). Regarding carotenoids, they are photosynthetic accessory pigments. They invariably increase under elevated UV-B (Kurinjimalar et al. 2019). UV-B radiation drastically affects the leaf thickness, morphology, and anatomy of plants, thus influencing plant photosynthesis (Wijewardana et al. 2016).

Gartia et al. (2003) registered a decline in the efficiency of photosystem II, while Kolb et al. (2001) reported no impact of UV-B on PSII. This contradiction in the impact of UV-B radiation on PSII needs further investigation. Enhancement in the UV-B-absorbing compounds in leaves like flavonoids, which act as a protective wall for sensitive targets, is a typical reaction to higher UV-B (Bassman 2004). Flavonoids are light-sensitive, so their concentrations are higher in plant cells subjected to UV radiation (Bilodeau et al. 2019; Liu

et al. 2020). According to Hada et al. (2003), anthocyanin did not cooperate in the UV-B protection system, while Gitz et al. (1998) reported that anthocyanin cooperates in the system that works to improve UV-B protection. The metabolism of amino acids may be affected by UV-B radiation, and it can induce protein biosynthesis in both the cytoplasm and chloroplast, which might help protect the plant against functional and structural impairments (Nedunchezhian et al. 1992). Yao and Liu (2007) documented that elevated UV-B radiation can inhibit photosynthesis in Gossypium sp., P. asperata while in Vitis vinifera, ambient UV-B is sufficient to hinder photosynthesis (Kolb et al. 2001). Variations in plant response to supplementary and ambient UV-B depend on the plants' sensitivities to UV-B (Tsormpatsidis et al. 2010). UV induces downregulation of genes encoding chlorophyll a and b binding proteins and causes damage in PSI and PSII. UV-B damages the D1 and D2 protein constituents of PSII (Hollósy 2002). Moreover, the other components are negatively affected by including quinone acceptors, reaction centres, and redox-active tyrosine (Hollósy 2002). In response to increased incident UVB radiation, many important photosynthetic genes exhibit reduced expression (Yadav et al. 2020).

Variations in secondary metabolites, photosynthetic pigments impairment due to oxidative stress (Kataria 2017; Escobar-Bravo et al. 2017), variations in cuticular wax deposition (Willick et al. 2017), disruption in the electron transport chain, and massive damage to PSI and PSII proteins (Rai et al. 2018; Zhang et al. 2016) are all harmful effects of UV-B. UV-B radiation has the ability to lower the maximum quantum yield of PSII (PSII max: Fv/Fm), a measure of the photosynthetic system's health in higher plants (Zhang et al. 2016). In addition, a significant decline in stomatal conductance (Gs) and generation of reactive oxygen species (ROS) were seen when plants were subjected to UV-B (Hideg et al. 2013; Tossi et al. 2014).

The increased ROS production, when exposed to UV, has been related to metabolic disturbance and escalated activity of membrane-localized NADPH-oxidase (Nawkar et al. 2013). IAA is a key plant hormone of the auxin class, and its deficiency reduces stem growth (Ros and Tevini 1995). UV-B potentially damages IAA and could down-regulate genes related to IAA activity (Ros and Tevini 1995; Pontin et al. 2010). According to Kataria et al. (2013), a decline in the activity of Rubisco in plants exposed to UV-B leads to reduced carbon dioxide fixation and oxygen generation. The chlorophyll content of wheat, sorghum, barley, cotton, and amaranth was reported lower when treated with UV-B than in controls (Klem et al. 2015). UV-B radiation causes lower specific leaf weights (Yao et al. 2008). UV-B radiation reduces stomatal conductance, altering leaf anatomy, and enhances leaf thickness (Bornman and Vogelmann 1991; Bornman et al. 1983). This change in the leaf architecture causes variation in light penetration into the leaf and hence alters the plant morphology (Hollósy 2002).

Photoperiodic response and UV-B radiation

Sunlight drives photosynthesis and provides vital environmental information, but it can also be an environmental stressor for plants due to high light and ultraviolet B (UV-B) radiation (Demarsy et al. 2018). Light information is obtained via specific photoreceptors, which influence plant metabolism, development, and viability throughout the life cycle (Jenkins 2017; Liang et al. 2018). Photoreceptor signaling frequently optimizes photosynthesis and safeguards plants from potential light stress (Demarsy et al. 2018). Diverse photoreceptors that recognize photons of specific wavelengths and transform them into cellular signaling cascades have evolved. Photoreceptor-mediated signaling allows plants to respond appropriately to changes in the light spectrum's, quantity, quality, direction, and duration (photoperiod).

These photoreceptors in flowering plants include the blue/ ultraviolet-A (UV-A) light-perceiving cryptochromes, phototropins, and Zeitlupe family members, the red/far-red lightperceiving phytochromes, and the UV-B photoreceptor UV Resistance Locus 8 (UVR8) (Galvão and Fankhauser 2015). UV-B exposure caused Arabidopsis plants grown in long days to flower later, owing to an effect on the age pathway (Dotto et al. 2018). RUP2 has been shown to play a repressive role in the regulation of photoperiodic flowering in the presence of UV-B (Arongaus et al. 2018). Intriguingly, rup2 mutants exhibit a day length neutral phenotype under UV-B and flower early under noninductive, short-day conditions in a UVR8-dependent manner (Arongaus et al. 2018). RUP2 interacts physically with the essential flowering inducer CO and inhibits the association of CO with the promoter of the flowering hormone FL (Arongaus et al. 2018). This mechanism counterbalances the potential early flowering induced by UVR8 in plants containing RUP2 so that these plants flower late under short-day conditions, providing a critical mechanism of photoperiodic flowering control (Arongaus et al. 2018).

Limited research has been conducted on the role of UV-B and/or UVR8 in regulating flowering time in plants (Zioutopoulou et al. 2022). Wild type Landsberg erecta (Ler) plants exposed to UV-B irradiation showed a delayed flowering phenotype, whereas uvr8 mutants flowered earlier than their wild type counterparts (Hayes et al. 2014). Furthermore, the UVR8-signaling trajectory has been linked to a delay in flowering time in the Arabidopsis Columbia-0 (Col-0) ecotype under short day (SD) and long day (LD) photoperiodic conditions. Flowering time analysis revealed that UVR8 did not reveal a significant difference in flowering time in response to WL (white light) supplemented with short-time interval high fluence rate UV-B in LD compared to a late flowering phenotype observed in Col-0 (Dotto et al. 2018). RUP2, a UVR8-repressor, has been shown to prevent CO from binding to the FT promoter, resulting in a significant delay in flowering time in plants grown under a SD photoperiod supplemented with UV-B (Arongaus et al. 2018).

Despite significant efforts to understand how UVR8 and UV-B regulate plant responses, the molecular mechanism by which the aforementioned factors regulate flowering time under LDs continues to remain largely unknown (Zioutopoulou et al. 2022). Zioutopoulou et al. (2022) demonstrated that constant low levels of UV-B (0.5 μ mol m⁻² s⁻¹) promote flowering initiation in Col-0 and Ler Arabidopsis ecotypes under LD photoperiodic conditions. UV-B also induces early flowering in mutants missing key flowering (co), UV-B (uvr8 and rup1rup2) and light signaling (cop1, pif4, and ztl) components. Moreover, they demonstrated that UVR8 functions as a negative regulator of UV-B-induced early flowering, as uvr8 mutants exhibited early flowering phenotypes when exposed to white light supplemented with UV-B. Overall, their findings showed that UV-B can influence flowering initiation at the transcriptional level via the action of UVR8.

Redox homeostasis and UV-B radiation

The sustenance of plant life in stressful environments is controlled at the cellular level by homeostasis in the usual redox reactions (Anjum et al. 2016). Redox reactions can produce a variety of reactive oxygen species (ROS). ROS, as integral signaling molecules, regulate plant growth and development as well as modulate their responses to abiotic and/or biotic stimuli (Baxter et al. 2013). ROS and their reaction products can modulate plant stress responses and/or severely impair cellular redox homeostasis beyond their steady-state cellular concentrations (Baxter et al. 2013). However, severe environmental conditions are unavoidable for plants and can over-oxidize or over-reduce the cellular environment. Plants are equipped with a number of mechanisms to proficiently metabolize and firmly regulate the steady-state levels of cellular ROS and its reaction products, as well as maintain optimal cellular redox homeostasis (Anjum et al. 2016). The major cellular redox homeostasis managers contain redox related components such as proteinaceous hiol members like glutaredoxin, thioredoxin, and peroxiredoxin proteins as well as crucial soluble redox compounds like ascorbate and glutathione (Anjum et al. 2016).

The radiation induces an imbalance between the energy absorbed through the photophysical process of photosystem (PS) II and the energy consumed for carbon assimilation. Decline in the primary photochemistry of PS II induced by UV-B in the background of relatively stable P_n , has been implicated in the creation of the energy imbalance. The

radiation induced damage of PS II hinders the flow of electron from Q_A to Q_B resulting in a loss in the redox homeostasis between the Q_A to Q_B leading to an accumulation of Q_A^- . The accumulation of Q_A^- generates an excitation pressure that diminishes the PS II-mediated O_2 evolution, maximal photochemical potential (F_v/F_m) and PS II quantum yield ($\Phi_{PS II}$). While UV-B radiation inactivates the carotenoid-mediated protective mechanisms, the accumulation of flavonoids seems to have a small role in protecting the photosynthetic apparatus from UV-B onslaught. The failure of protective mechanisms makes PS II further vulnerable to the radiation and facilitates the accumulation of malondialdehyde (MDA) indicating the involvement of reactive oxygen species (ROS) metabolism in UV-B-induced damage of photosynthetic apparatus (Joshi et al. 2011).

The uneven destruction of these photosystems is likely to result in an energy imbalance that causes a loss of redox homeostasis in the photosynthetic apparatus, a possibility that has not been investigated in detail (Joshi et al. 2011). In addition, the majority of findings regarding UV-B effects on photosynthetic apparatus are based on reductionist studies, and no effort has been made to evaluate both primary photochemistry of thylakoids and carbon assimilation in the Calvin-Benson cycle in a single plant system in order to determine the relative susceptibility of various major components of chloroplasts to UV-B radiation (Joshi et al. 2011). The simultaneous study of primary photochemistry and carbon assimilation allows for the analysis of UV-B-induced changes in the efficiency of electron source and electron sink capacity, which may lead to an energy imbalance in photosynthetic apparatus (Joshi et al. 2011). High UVB doses induce the oxidation of biomolecules like proteins, phospholipids, and nucleic acids, which causes severe cell damage in plants (Cassia et al. 2019). Low UVB doses function as signaling molecules, effectively regulating cellular redoxhomeostasis (Yokawa et al. 2016). Relevant literature discloses that UV-B radiation causes damage to green plants' photosynthetic apparatus at numerous sites. The sites of damage include oxygen evolving complex, D1/D2 reaction centre proteins and other components on the donor and acceptor sides of PS II (Brosché and Strid 2002). Additionally, the radiation deactivates the xanthophyll cycle related with light harvesting complex II and modifies gene expression for the synthesis of PS II reaction centre proteins (Brosché and Strid 2002). Even ambient UV-B radiation has deleterious effects on the photosynthesis of Arctic plants and algae (Albert et al. 2011; Roleda et al. 2009), in addition to altering their ultrastructure, growth, respiration, and reproduction (Roleda et al. 2009).

Electron carriers and energy metabolism mediators like non-phosphorylated (NAD⁺) and the phosphorylated (NADP⁺) coenzyme forms and their redox couples GSSG/ GSH, DHA/AsA NAD⁺/NADH, and NADP⁺/NADPH also play a role in cellular redox homeostasis (Suzuki et al. 2011; Giordano 2013). Cellular redox homeostasis has also been identified as the primary "integrator" of information derived from metabolism and the plant-environment interaction (Foyer and Noctor 2009). Thus, uncovering insights into the role and primary mechanisms of redox homeostasis in plants under environmental stresses should be the principal focus of present-day plant research.

UV-B radiation effect on major cereals

UV-B radiation and wheat

C3 crops like wheat, cotton, and soybeans are generally considered more susceptible to UV-B radiation than C4 plants (Gao et al. 2003). Reduction in biomass and yield under controlled environments due to UV-B is mainly associated with its detrimental impacts on plant photosynthetic pigments (Alexieva et al. 2001) and the photosynthetic rate of the leaf (Hideg et al. 2006). Studies reported the pernicious impacts of ambient and enhanced UV-B radiation on the photosynthetic system in wheat, i.e., the efficiency of PS II, the thylakoid, and CA, MDH, Rubisco, PEPC, and chlorophyllase enzymes (Kataria and Guruprasad 2012; Chen and Han 2014; Kataria et al. 2013). Feng et al. (2007) found that increased UV-B delayed phenology, decreased pigment contents such as chlorophyll a and b, and decreased photosynthetic capacity, root, stem, and leaf biomass, yield, water potential, and relative water content of wheat leaves. Additionally, a rise in membrane permeability and UV-B absorbing compounds like flavonoids was observed. Reductions in photosynthetic performance, biomass, and growth in wheat seedlings were recorded due to ambient and supplemental UV-B radiation (Liu et al. 2015; Kataria and Guruprasad 2015).

Furthermore, changes in shoots, plant dwarfism, and a reduction in the width and length of leaves in wheat seedlings were reported when subjected to UV-B radiation (Liu et al. 2015). These changes are related to alterations in cell division or elongation (Singh et al. 2014a). Ran et al. (2018) also documented that UV-B radiation caused significant modifications in the root length, number, biomass, and vigour of wheat.

The grain yield of wheat was reduced by 18–57% due to higher UV-B when stratospheric ozone reduction was assumed at 12–25%, along with a reduction of 30% in its thousand-grain weight (Li et al. 2010). Hakala et al. (2002) reported that enhanced UV-B radiation had no significant effect on wheat grain yield. Wheat phenophases and their sensitivity to a higher level of UV-B are critical for determining wheat performance in the future because biomass partitioning, and yield production depend on developmental stages (Slafer et al. 2019). Lizana et al. (2009) documented a decline of 11–19% in biological and 12–20% in grain yield of wheat with higher UV-B at the 3L-Bo phase, but no influence was recorded with higher UV-B in the later stages. No significant effect on the biological and grain yield of wheat was observed when subjected to a higher UV-B level in field conditions (Ambasht and Agrawal 2003).

Several studies regarding the effect of UV-B on the grain quality of wheat have been conducted, but the results found are contrasting. Zu et al. (2004) reported a positive effect, while Calderini et al. (2007) documented no influence of UV-B radiation on the grain protein content in wheat. Zu et al. (2004) reported that the response of wheat varieties to UV-B radiation differs in terms of quality, like amino acids or total sugar content. The decrease in quality and yield of wheat when exposed to enhanced UV-B radiation will have serious economic and nutritional consequences (Li et al. 2010). Figure 5 depicts the impact of enhanced UV-B on wheat performance.

UV-B radiation and maize

Crops, including maize grown between 40°N and 40°S (latitudes), facing 2-10 (kJ m⁻² d⁻¹) UV-B based on season and location (Reddy et al. 2013). Maize is seriously affected by abiotic stresses, including UV-B radiation, which are estimated to intensify in the future. Maize is sensitive to higher UV-B radiation (Yin and Wang 2012) and increased UV-B radiation significantly reduced dry matter accumulation, grain yield, chlorophyll a, and b, and caused a decline in protein, starch, and sugar content of maize seed, while a significant increase in flavonoid accumulation and lysine content was reported under higher UV-B treatment (Gao et al. 2004). Singh et al. (2014b) registered that higher UV-B radiation did not affect chlorophyll and carotenoid concentration in maize leaves, while plant growth was negatively affected by UV-B. Maize undergoes early senescence with lower photosynthesis when treated with higher UV-B concentration (Correia et al. 2005). Reddy et al. (2013) documented that both ambient and predicted UV-B levels could influence maize growth by negatively affecting the stem extension, leaf area development, photosynthesis, and eventually biomass. UV-B radiation has a negligible effect on leaf appearance and the susceptibility of each developmental phase to UV-B radiation in maize varies from hybrid to hybrid (Reddy et al. 2013).

UV-B radiation is one of the major stresses significantly affecting maize yield (Wijewardana et al. 2016). Several researchers (Ballare et al. 2011; Kim et al. 2007; Yin and Wang 2012) reported that crops, including maize, when exposed to higher UV-B levels showed an extensive decline in quality and yield, indicating that maize is sensitive to a higher dose of UV-B radiation. A rise of 9.5% in UV-B decreased the protein content of maize by 33% (Gao et al.



Fig. 5 Impact of greater UV-B on photosynthesis, growth, and antioxidants (Häder et al. 2015)

2004). Yin and Wang (2012) recognized that the growth and yield of maize were harmfully affected by enhanced UV-B radiation and the reduction in yield was due to the fewer seeds per row and seed weight.

Moreover, exposure to higher UV-B increased the protein content with no effect on starch and oil contents, showing both the positive and negative impacts of higher UV-B radiation on maize. Higher UV-B treatment at silking enhanced N concentration in stems and leaves, K, Zn, and Ca in stem while UV-B showed no effect on Mg, Fe, P, Mn, and Cu concentration (Correia et al. 2012). Moreover, P declined in almost all plant organs, Mn decreased in grains and leaves, while Zn, Mg, and Ca increased in stem and grains. Cu concentration increased when maize was treated with enhanced UV-B at harvest maturity (Correia et al. 2012). They further reported a slight rise in NUE with higher UV-B treatment, although this increase was not significant. Though higher UV-B radiation decreases nutrient uptake, the studies did not show any critical nutrient limitation in plants treated with higher UV-B (Correia et al. 2012).

Likewise, Zancan et al. (2006) reported that Fe content in leaf and root increased in maize under greater UV-B. Additional UV-B radiation significantly reduced the dry matter and yield of maize along with its effect on seed quality i.e., starch, protein, and sugar levels decreased, however, the lysine level was found to be improved (Gao et al. 2004).

UV-B radiation and rice

Rice is grown in tropical regions, receiving more UV radiation because of higher solar angles. Most developing countries fall in this region (Wagh and Nandini 2019). Enhanced UV levels caused chloroplast destruction (De Almeida et al. 2012), a decline in photosynthetic capacity, thus significantly reducing grain size, panicle number (Hidema et al. 2006), total biomass, and tiller production in rice (Mohammed et al. 2007). In rice, enhancement in the degradation of Rubisco was observed at leaf maturation when supplemented with UV-B radiation (Takeuchi et al. 2002). Wagh and Nandini (2019) documented that with an increase in UV-B, the morphological traits (like plant height, and tiller numbers), physiological traits (like leaf gas exchange and chlorophyll content) decreased significantly while protective compounds like flavonoids and catalase increased and the combined effect of these components were noticed as a decline in grain yield in rice. Rice exposed to a prolonged period of enhanced UV-B resulted in spikelet sterility (Mohammed and Tarpley 2010).

Li et al. (2019) reported that in rice, the blast disease index was significantly reduced with an increase in UV-B radiation, but as the infection increased, the inhibitory effect due to UV-B on this disease was weakened. Storage proteins, particularly glutelin and total N increased under supplemental UV-B radiation in rice (Hidema et al. 2006). The taste of the rice grain could be changed when subjected to UV-B radiation (Hidema and Kumagai 2006). Ling et al. (2022) reported that the content of gibberellin and brassinolide in rice flag leaves increased by 60.1% and 29.94%, respectively under elevated UV-B when compared to natural light. However, the content of auxin decreased by 17.3% under increase UV-B. A summary of the various physiological and biochemical responses of the cereals is displayed in Table 3.

Interaction between UV-B radiation and other abiotic stresses

In the natural environment plants usually have to deal with continuous variations in light quality and intensity along with variations in other abiotic factors like increased CO_2 , temperature, and water shortage, among others which have both positive and negative effects on plants (Table 3). Sicora et al. (2006) concluded that PSII of the photosynthetic apparatus is highly sensitive to UV-B radiation. Conversely, because of its very effective repair system, impairment of this component becomes limiting for photosynthesis only when its repair capacity is reduced by other stresses like drought, higher temperatures, high-intensity visible light, etc. Hence, the plants subjected to UV-B under other environmental stresses, which slow down the repair of PSII which can limit the production of NADPH and ATP needed for the Calvin cycle and ultimately for the overall process of photosynthesis. Several researchers have acknowledged the main effect of UV-B radiation and temperature on plants however; limited studies describe their mutual effects on plant chemistry and physiology (Escobar-Bravo et al. 2017). Mostly, these studies examined a compensatory effect of higher temperatures on plant growth inhibited due to UV-B radiation (Escobar-Bravo et al. 2017) (Table 4).

Mark and Tevini (1996) in their study on sunflower and maize reported that a rise in temperature from 28–32 °C increased the growth parameters irrespective of the UV-B treatment. Furthermore, they reported that the adverse effect of UV-B radiation on plant growth was compensated by the higher temperatures. Likewise, Han et al. (2009) also reported that enhanced UV-B radiation caused a reduction in photosynthesis rate, chlorophyll content, and plant growth in the seedlings of dragon spruce (*Picea asperata*) but these negative effects were compensated by higher temperature. While pre-exposure to ambient and low amounts of UV-B enhanced heat resistance in conifer seedlings (L'Hirondelle and Binder 2005) and cucumber (Teklemariam and Blake 2003).

The interaction between drought and UV-B radiation in plants has received attention in recent years; however, the mechanism of tolerance or sensitivity to their combined effect has not been studied in detail and still needs more research (Zlatev et al. 2012). Uncovering drought and UV-B interaction would provide useful insights to understand the possible outcomes of stratospheric ozone depletion on an adaptation of plants to environmental shifts. When drought stress and moderate UV-B occur simultaneously, they can work synergistically to boost plant resistance and ultimately plant survival. These responses were related to higher production of UV-B absorbing compounds, antioxidant proteins, and leaf cuticle thickness (Bandurska et al. 2013). In wheat seedlings, UV-B radiation and drought stress caused higher H₂O₂ accumulation leading to lipid peroxidation and reduction in growth. Moreover, it was concluded that combined stress affected more negatively plant growth than individual stress factors (Tian and Lei 2007). Feng et al. (2007) recorded that photosynthetic capacities, plant growth, pigment contents, and yield of wheat were reduced when both UV-B radiation and drought stress treatments were applied mutually in comparison when stresses were applied separately. Combined UV-B radiation and drought stress caused a reduction in chlorophyll content and photosynthetic capacity in both soybean and maize, thus resulting in lower total dry matter production (Shen et al. 2015).

Environmentalists are concerned about the widespread use of herbicides and pesticides in agriculture (Ashry et al. 2018; Ahmad et al. 2021a, b). Herbicides used in agriculture are transported to bodies of water via run-off, drift, and leaching, increasing the risk of exposure in non-target organisms (Chen et al. 2007). Some herbicides cause metabolic changes in algae as a result of oxidative stress (Romero et al. 2011), while others work by binding to the exchangeable quinone site in the photosystem II reaction center, thereby blocking electron transfer (Rutherford and Krieger-Liszkay 2001) or by altering the fluorescence emission and electron transport activities of the bio-samples (Ventrella et al. 2010). UV radiation has also been shown to promote the breakdown

 Table 3
 Physiological and biochemical responses of cereals to higher UV-B radiation

Crop	Response	References
Wheat	Stunted growth	Kataria et al. (2019)
	Reduced rate of photosynthesis	
	Increased anti-oxidant defense	
	Reduced DNA, RNA, protein	
	Low PS II quantum yield	
	Decrease activity of Rubisco	
	Reduced thylakoid and enzymes like Rubisco, carbonic anhydrase (CA), malic dehydroge- nase (MDH), PEPC, and chlorophyllase	
	Reduced grain yield	
	Decreased the indole-3-acetic acid content	Li et al. (2010)
	Reduced chlorophyll fluorescence yield	Kataria and Guruprasad (2015)
	A decline in ascorbic acid	Agrawal and Rathore (2007)
	High H ₂ O ₂ accumulation	Chen et al. (2019)
	Excessive ROS generation	Tian and Lei (2007)
	Changes in the content of amino acids, proteins, and total sugars of wheat grain	Yavaş et al. (2020)
	Increased phenolic content and antioxidant activity	Chen et al. (2017)
	Malondialdehyde content in the leaves of wheat seedlings significantly increased Significant reduction of SOD (superoxide dismutase) Increased CAT activity	Liu et al. (2012)
	Changes in the molecular structure of the starch	Nowak et al. (2023)
	Decreased phytosiderophore release and root Fe accumulation	Wong et al. (2023)
Maize	Reduced PEPC and Rubisco enzymes activities	Correia et al. (2005)
	Increment of proline	Carletti et al. (2003)
	Inhibits maize leaf growth	Fina et al. (2017)
	Reduction in plant total leaf number Increase in the production of epicuticular wax	Wijewardana et al. (2016)
	Gibberellins concentration reduces	Fina et al. (2017)
	Ribosome damage Decrease in translation in RNA of maize	Casati and Walbot (2004)
	Levels of protein, sugar, and starch in maize seed decreased The level of lysine increased Flavonoid accumulation increases Reduced the dry matter accumulation	Gao et al. (2004)
	Increase of the iron content in both roots and leaves	Zancan et al. (2006)
	Reduced leaf area and leaf thickness	Kataria and Guruprasad (2012)
	Decreased chlorophyll	Jovanić et al. (2022)
Rice	Variations in IAA and ABA phytohormones	Huang et al. (1998)
	Reduction in photosynthetic activity	De Almeida et al. (2012)
	Decreased rubisco activity, content, and electron transport rate	Fedina et al. (2010)
	Increased antioxidant activity	Ti et al. (2014)
	Carotenoid content increased MDA content significantly increased Enhanced total phenolic content Ascorbate content increased Increased proline content High SOD activity (superoxide dismutase)	Faseela and Puthur (2019)
	Increase in protein	Du et al. (2011)
	Fe content decreased in leaves Mn, Cu content increased in root and leaves Reduced chlorophyll and carotenoid	Lidon (2012)
	Accumulated antioxidants and proanthocyanidins content	Li et al. (2023)

Table 3 (continued)

Crop	Response	References
Barley	UV-B treatment accumulated phenolic acids and antioxidant enzyme	Wang et al. (2022)
	Reduced grain yield	Tsygvintsev et al. (2019)
	Effect on germination rates	Lazim and Ramadhan (2020)
	UV stress could efficiently improve/preserve the contents of total polyphenols, total flavo- noids, total triterpenes, total polysaccharides, proanthocyanidins, chlorophyll <i>a</i> , chloro- phyll <i>b</i> , and total chlorophyll, as well as the OH [•] and ABTS scavenging	Jiang et al. (2020)

 Table 4 References indicating the positive and negative interactions of stress combination

	Stress combination	References
Positive interaction	Ozone + UV	Mittler and Blumwald (2010)
	Pathogen+UV	Bowler and Fluhr (2000)
Negative interaction	Drought+UV	Bandurska et al. (2013)
	Heat + UV	Mittler and Blumwald (2010)
	UV + Heavy metals	Srivastava et al. (2012)

of many pesticides including fenitrothion (Weber et al. 2009) and triazophos (Leach et al. 2017). Increased UV-B radiation reduced the effectiveness of paraquat by increasing leaf wax content and inhibiting photosynthesis (Wang et al. 2007). Because paraquat's mechanism of action is closely correlated to light, the impacts of increased UV-B radiation on paraquat performance may differ from its impact on other herbicides with different modes of action.

Glyphosate is more extensively used and has a different mode of action than paraquat. Glyphosate's mode of action involves blocking the production of the enzyme 5-enolpyruvylshikimate-3-phosphate (EPSP) synthase (Yin et al. 2012). In their study, Yin et al. (2012) found that the effectiveness of glyphosate decreased with enhanced UV-B radiation because of changes in absorption, translocation, and distribution which were attributed to a higher leaf-surface wax and photosynthesis inhibition by elevated UV-B radiation. Furthermore, they suggested that the negative effects of increased UV-B radiation on herbicide efficacy could be widespread. Therefore, additional research is required to confirm the aforementioned results and investigate the impact of elevated UV-B radiation on herbicide application technology (Yin et al. 2012).

Heavy metals when combined with other abiotic stresses also have a harmful effect on plant growth and development (Akladious and Mohamed 2017; El-Mahdy et al. 2021; Abu-Shahba et al. 2022). UV-B radiation alone or Nickle inhibited the growth in the root and shoot of pea seedlings, but their combined effect resulted in more serious damage (Srivastava et al. 2012). Additionally, their combined effect reduced carotenoid concentration and might also have a deleterious effect on chlorophyll and photosynthesis (Srivastava et al. 2012). In natural habitats, the impact of UV-B radiation on plants is closely associated with other factors like higher temperatures, drought, heavy metals, CO_2 , and ozone. Therefore, future studies and improved insight into the interaction between UV-B radiation and other environmental stresses would greatly allow determining more realistically the impact of increased UV-B radiation in the presence of other stress factors.

Future prospects

Plants are sessile and cannot escape from UV-B radiation from the sun. Many organisms, including plants, are affected by changes in UV-B radiation and other environmental stresses produced because of climate change. The changes occurring due to climate change will continue and will, directly and indirectly, affect agricultural production by affecting plant performance. In this scenario, a significant research gap is how crops particularly major food crops react to changes in UV-B radiation in the presence of other several environmental stresses. Besides ozone depletion, climate change also significantly changes the amount of UV radiation reaching the earth's surface. Therefore, a novel approach to studying the role of UV-B radiation in the context of climate change is of utmost importance. Research showed that UV radiation and other stress factors are modifying plant responses, but further understanding of these modifications is necessary to classify them as positive or negative to make possible future projections. A knowledge gap exists regarding the impact of UV-B radiation in the presence of other stresses, and research that encompasses realistic conditions is required for future projections. This paper has summarized some impacts of UV-B radiation on plants, but further studies are also needed to evaluate the role of UV-B radiation in the background of climate change. More long-term experiments under open conditions need to be designed to fully disclose the interactive effect of UV-B radiations and other stresses on crop response.

Among other drastic effects of climate change on agriculture, a rise in UV-B radiation due to ozone depletion is also a result of climate change. The rise in the emission of GHGs due to anthropogenic activities is reducing the ozone layer and providing a path for UV-B radiation to reach the earth's surface and interfere with agriculture. Enhanced UV-B affects plant morphology, physiology, biochemistry, and ultimately the yield negatively. Ozone is depleting, and UV-B radiation is increasing; thus, the role of plant physiologists and breeders is vital in introducing new cultivars having traits to tolerate a higher level of UV-B under changing climate to compensate for the yield losses. There are limited studies reporting the impact of enhanced UV-B on the performance of major food crops. The available literature is not enough to generalize the effects of UV-B on plant performance. How crops will respond to elevated UV-B in the presence of many other environmental stresses is a major research gap. Further studies related to the impact of UV-B radiation in combination with other biotic and abiotic stresses emerging due to climate changes are recommended to assure high yield from the crops in the future and better understand the interaction of these various stresses. There isn't enough information about the potential to exploit plant UV-responses in climate change resilience breeding programs (Robson et al. 2019). In this regard, plant biotechnological approaches will provide improved breeding programmes to produce UV-B tolerant cultivars like using QTL mapping for genetic markers conferring resistance to UV-B radiation. Similarly, using crop transformation approaches like CRISPR/Cas9, molecular assisted genetic engineering will also assist in overcoming abiotic stresses like elevated UV-B radiations. Quantifying the simultaneous effect of UV-B radiation and other stresses on plant performance is challenging but is of paramount significance.

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