Significance of UV-B Priming in Agricultural Crops : A Review

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Priyanka Uniyal : Conception & design, data collection, data analysis and interpretation
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Received : April 2022
Accepted : July 2022

Abstract

The tremendously growing global human population and increasing level of UV radiation necessitates the need for developing a cost-effective, convenient and environment-friendly method for improving the quality and quantity of food crops. UV-B radiation has particular regulatory functions in plant growth and development, which can lead to increased plant hardiness, increased plant resistance to herbivores and diseases and improved agricultural product quality, all of which have implications for food security. UV-B priming is one of the most efficient techniques helpful in increasing yield and improving quality of the crop. The review paper scrutinizes the previous research studies on effect of UV priming on plants, mainly focusing UV-B priming. The overall significance of this technique and the mode of action through which the photomorphogenic responses are brought about in plants after UV exposure are discussed in detail. We found certain gaps in research that are needed to be addressed. Exposing plants to low doses of UV-B increases the production of antioxidants, phenolics, pigments and enzymes, overall strengthening defense system and increasing the efficiency of photosystem of the plant. Experiments on the effects of UV-B light needs precise monitoring of UV radiation. The development of tools and procedures that permit for the estimation of pragmatic UV radiation exposures of discrete plants, natural ecosystems and agricultural contexts need further attention. Ecologists are to forecast the expected effects of natural ecosystems; investigations of the combined effects of environmental variables and UV-B radiation will be required for the development of stress-tolerant crop varieties. A better understanding of the mechanism of UV-B priming mechanisms will aid in the development of seed production technologies. The role of UV-B photo receptor, *UVR8*, in nucleoplasmic gene transcription and the link between *UVR8* activation and repression of hormone production or signaling are all questions that needs to be explored further.

Keywords : Abiotic stress, Agriculture, Crop production, Photoprotection, UV priming, UVR8

There is an exponential rise in global human population over the last few decades resulting in increased demand for higher crop production to provide ample food for everyone. A slow decline in the growth rate of agricultural crops has been observed due to excessive use of different agro chemicals and fertilizers and also because of intensive conventional breeding of high yielding crop varieties (Godfray *et al.,* 2010). There is a global search for effective, sustainable and economic technologies that may help to cope with a perceived food supply problem and also to counter various environmental stresses.

Studies have shown that the main contributors to reduction in cultivated crop production are various environmental abiotic and biotic stresses such as very high or low temperature, high salinity, mineral deficiency, drought, water logging, increased solar UV radiation, pathogens, herbivores, weeds etc. (Slama *et al.,* 2015 and Zhu, 2016). These stresses may trigger oxidative stress in plant aided by the over-production of Reactive Oxygen Species (ROS), as a result promoting denaturation of protein, lipid peroxidation and nucleotide degradation, along with intense cellular damage and cell death eventually (Thomas *et al.*, 2020). Plants employ scavenging mechanisms, like superoxide dismutase (SOD), ascorbate peroxidase (APX), catalase (CAT) and glutathione peroxidase (GPX), which scavenge ROS and hence enhancing tolerance to stress (Chen *et al.,* 2016 and Raja *et al.,* 2017).

Increased solar UV radiation due to attenuation of stratospheric ozone layer is one of the important environmental stresses governing the distribution of plants on Earth. Exposure to biologically-effective levels of UV radiation is certainly not harmful if plants are successfully acclimatized, which depends on different environmental conditions like climate variables, latitudinal location etc. (Comont *et al.,* 2012) and plant type. UV radiation is also an important regulator of morphological, physiological, biochemical and genetic processes in plants, making it useful to exploit for improving agricultural crops (Wargent *et al.,* 2011). High UV-B levels will initiate signaling responses that may help in acclimation and survival of a plant (Hideg *et a*l., 2013). Plants can become more robust through UV exposure (Zhang and Björn, 2009).

Priming refers to the process of acclimatizing a plant by exposing to low doses of an abiotic stress, thereby providing stress tolerance along with certain beneficial properties to the plant (Wargent and Jordan, 2013). Priming of a plant can be done at two stages, *i.e.,* seeds and seedlings, out of which seed priming is more convenient and effective for providing stress tolerance (Jisha *et al.,* 2013).

This method of preparing plants helps to meliorate crop quality and production even under stressful environment, thus providing better agronomic gain. The idea of putting UV radiation to use as a priming agent has garnered copious attention and several reports have discussed its beneficial influence on plant (Hideg *et al.,* 2013; Wargent & Jordan, 2013 and Bornman *et al.,* 2015). The overall objective is to augment the quality or quantity of the yield and develop the stress-tolerant quality crops by exposing to mild dose of biologically effective UV radiation (Martinez *et al.,* 2018). Moreover, UV priming serves as an environmental-friendly method to enhance total crop yield and also for building stress tolerance in plants (Badridze *et al.,* 2016).

In the present review, we have investigated into UV priming in detail, primarily focusing on UV-B priming. The review discusses the earlier studies, types of priming, mode of action and significance of UV priming. We also identified some voids in the research knowledge and approach. In conclusion, we have provided some suggestions for research that may help fill the lacuna in information.

Mode of Action

It is a known fact that UV-B can induce either stress responses or photomorphogenic responses in plant. The stress responses are due to high fluence rate of exposure to UV-B while controlled low fluence rate of exposure brings about positive results to the crop. Although there are enough research studies to prove the benefits of UV priming in improving crop quality and production, the exact mechanism behind regulation of photomorphogenic responses by UV exposure is yet not well understood. Scientists believe that there are highly specific signaling molecules responsible for bringing the photomorphogenic responses through UV-B in plants. Researchers have investigated the action mechanism of UV radiation at molecular level in mainly two plants, *i.e., Arabidopsis thaliana* and *Zea mays*. The three key regulators involved in UVB signaling in plants were identified as - *UV RESISTANCE LOCUS 8 (UVR8)*, *CONSTITUTIVELY PHOTOMORPHOGENIC 1 (COP1)* and bZIP transcription factor *ELONGATED HYPOCOTYL 5 (HY5)*. *COP1* regulates various other photo-responsive gene expressions, as arbitrated by UV-B exposure, besides flavonoid accumulation and restraining hypocotyl elongation. *HY5*, alongwith regulating many different photomorphogenic pathways, also helps in UV-B-induced gene expression (Oravecz *et al.,* 2006 and Brown & Jenkins, 2008).

Kliebentein reported the presence of *UVR8* as a signaling component which acted solely in the regulation of UV-B-specific gene expression (Kliebenstein *et al.,* 2002). Researchers found that UV-B irradiation actually redistributes *UVR8* molecules in the cell. The UVR8 photoreceptor upregulates the activity of UV target gene *CHALCONE SYNTHASE (CHS)*, which is the major regulatory gene in flavonoid biosynthetic pathway, responding quickly after exposure to UV radiation.

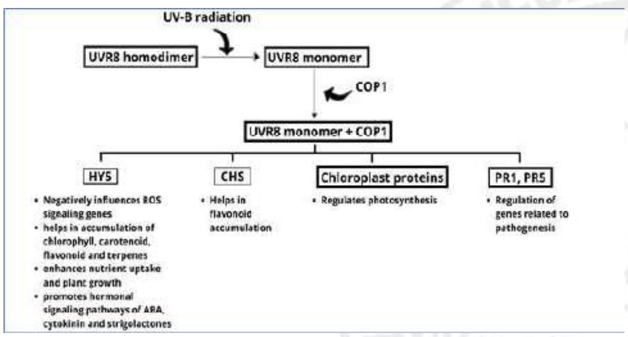

Fig. 1 : Possible action mechanism of UV-B priming in plants

Fig. 1, The possible mode of action of UV-B on plants. On the absorption of UVB photon, *UVR8* homodimer dissociates into *UVR8* monomers and interacts with downstream signaling factor *COP1* (Ulm and Jenkins, 2015). *UVR8* molecule dissociation takes place after just a brief exposure to UV-B and happens at low, physiological fluence rates, causing transcriptional modifications. The combined effect of *UVR8* and *COP1* causes the expression of a number of genes that protect plants from UV-B damage, such as genes encoding flavonoids biosynthesis enzymes, DNA repair enzymes and proteins involved in oxidative stress mitigation, as well as other photomorphogenic responses in plants.

Of these transcriptional factors, *HY5* transcription factor is the most important for regulating genes involved in photomorphogenic UV-B response. It is the centre of transcriptional network that modulates photomorphogenesis. *HY5* alongwith HYH interacts with *PHYTOCHROME INTERACTING FACTOR* (*PIF1* and *PIF3*) and negatively influences the expression of ROS signaling genes (Chen *et al.,* 2013). *HY5* promotes photomorphogenesis by modulating signaling pathways of hormones like cytokinin, abscisic acid (ABA) and strigolactones and suppressing signaling of hormones like auxin, gibberelin (GA), ethylene and brassinosteroid (BR). *HY5* is also involved in accumulation of flavonoids, carotenoids and chlorophylls (Toledo-Ortiz *et al.,* 2014). *HY5* inhibits hypocotyl elongation and lateral root development and promotes plant growth by inducing nutrient uptake (Gangappa and Botto, 2016). Moreover, *UVR8* is found to be engaged in pathogenesis-related genes regulation and modulating chloroplast proteins. *UVR8* increases the expression of PATHOGENESIS-RELATED (PR1 and PR5) proteins. *UVR8* also influences photosynthesis under UV-B radiation by regulation of genes encoding chloroplast proteins (Davey *et al.,* 2012).

Earlier Studies

Most of the earlier studies on effects of UV radiation on crop plants observed detrimental effects on the overall yield of the crops studied (Teramura, 1983). Most of these experiments used unfiltered sunlamps (BZS-CLG, FS-40 and Philips 40/12) that emitted very high UV enhancements, more than normal incident radiation in the field and also included UV-C radiation which is usually blocked by the ozone layer when comes from the Sun. Majority of the enhanced UV radiation studies done on different plants, which have shown damaging effects of exposure to UVB, have actually been a result of employing unusually high UV fluxes (Allen *et. al.,* 1998). Moreover, the sudden UV exposure of plants during these experiments seems unreal as compared to the prolonged natural exposure conditions. In contrast, normally incident UV radiation coming from the Sun is unlikely to cause severe damage and may help in photoprotection of photosystem of plants under stressful climatic condition.

Bartholic *et al.* conducted an interesting experiment growing 3 crops, *i.e.,* corn, bean and tomato, under UV lamps covered with either UV-B absorbing (Mylar) or UV-B transmitting (polyethylene) films (Bartholic *et al.,* 1975). They observed significant increase in yield in corn under the polyethylene panels. The other two showed no yield difference. Biggs and Kossuth studied the effect of increasing levels of filtered irradiances in 9 crops (Biggs and Kossuth, 1978). Total yield was seemed to remain unaffected in 5 out of 9 crops (corn, rice, radish, peanut and potato) and not significantly decreased in rest of the crops (tomato, pea, squash and mustard). There was some evidence of qualitative changes in potato tuber and size of fruit in peanut. Some species are resistant to UV-B radiation, most are sensitive, while growth in others is evidently increased.

Most of the earlier studies on effect of UV-B radiation on plants have frequently concluded UV-B as a threat to plants causing growth inhibition, particularly reduced leaf number and reduction in growth rate (Krizek *et al.,* 1998). But simultaneous increase in leaf thickness may compensate for the loss in leaf area via enhanced RuBisCo concentration per unit leaf area, which indirectly contributes to enhanced photosynthetic ability of the plant by increasing the total leaf volume (Wargent and Jordan, 2013). There are these various factors, such as the amount of UV-B dose, no. of doses per day, duration of UV-B exposure, developmental stage of the plant etc., that govern whether exposure to such radiation will prove to be detrimental or beneficial overall. Researchers noted elevation in net photosynthetic rate after exposing young *Lactuca sativa* seedlings to ambient UV-B levels during the early developmental stage, while sudden exposure to the same dose of UV-B during final developmental stage of the plant resulted in decline growth rate comparatively (Wargent *et al.,* 2011). They further confirmed through other observations that early exposure to UV-B may prove to be beneficial for providing photoprotection to plants. Some researchers have discussed that the pre-exposure of plants to low doses of UV-B will generate various photoprotective responses, such as thickening of epidermal waxy layer, increased production of phenolics etc., which in turn protect the photosystem competency of leaves from damaging effects of high frequency light (Hakala-Yatkin *et al.,* 2010).

The potential of UV exposure for enhanced production of certain beneficial biochemical compounds, such as antioxidants (Agarwal, 2007), alkaloids (Ramani and Chelliah, 2007) and glucosinolates (Reifenrath and Müller, 2007), is significant to note. One of such important biochemical compounds is phytoalexin 3, 5, 4' - trihydroxystilbene, commonly called resveratrol, *viz.,* used to be frequently isolated from the skin of red grapes (*Vitis vinifera*) (Moreno-Labanda *et al.,* 2004). The use of this compound for the treatment of obesity, ageing disorders and especially cancer has been a debate for long (Baur and Sinclair, 2006). The genes responsible for the biosynthesis of stilbene synthase, an important precursor to resveratrol production in plants, is upregulated by UV exposure on plants (Wang *et al.,* 2010). Table 1, summarizes some of the important research studies that prove the positive effects of UV-B priming on plants.

Types of UV Priming

Plants are shown to be best primed at early developmental stages of the life cycle. Hence, there are mainly two kinds of UV priming - seed priming and seedling priming. UV priming of plants at seed and seedling stages was shown to bring about many advantageous changes in different crop plants, like *Vigna unguiculata* (Mishra *et al.,* 2008), *Phaseolus vulgaris* (Kacharava *et al.,* 2009 and Aboul Fotouh *et al.,* 2014), *V. mungo* and *V. aconitifolia* (Dwivedi *et al.,* 2015) and *Trigonella foenum-graecum*, sugar beet and red cabbage (El-Shora *et al.,* 2015).

Out of these two types of UV priming, seed priming is extensively adapted by researchers for getting the best results with low risk of damages. Seed priming has been assumed to be more efficient, economic and convenient method for inducing stress tolerance in plants. Plants from primed seeds usually respond

TABLE 1

Research studies by several workers showing beneficial results of UV-B priming

Crop used	Changes observed	Reference
Brassica napus L.	Increased soluble flavonoids	Olsson *et al.,* 1998
Pseudotsuga menziesii (Mirb.) Franco	Increased rate of photosynthesis	Poulson *et al.,* 2002
Cucumis sativus L.	Increases vegetative growth	Teklemariam & Blake, 2003
Glycine max (L.) Merr.	Increased flavonoids, Superoxide dismutase (SOD) enzyme activity	Yanqun *et al.,* 2003
Triticum aestivum L.	Increase in protein content, total sugar content, total amino acids and grain quality index	Zu *et al.,* 2004
Hordeum vulgare L.	Enhanced rate of photosynthesis	Hideg *et al.,* 2006
Oryza sativa L.	Tolerance to photoinhibition, higher chlorophyll concentration, and higher photosynthetic activity	Xu and Qiu, 2007
Fagopyrum esculentum Moench	Increase in crop yield and plant height	Yao *et al.,* 2007
Vigna unguiculata (L.) Walp.	Increased carotenoid content	Mishra *et al.,* 2008
Momordica charantia L.	Increased carotenoids; increased enzyme activities of Superoxide dismutase (SOD), Catalase (CAT), Peroxidase (POX)	Mishra *et al.,* 2009
Triticum aestivum L.	Enhanced abscisic acid content, stomatal conductance, rate of transpiration and intracellular CO_2 concentration	Li *et al.,* 2010
Zea mays L.	Enhanced rate of seed germination	Wang *et al.,* 2010
Lactuca sativa L.	Enhanced photosynthetic rate, Improved photosystem II efficiency	Wargent *et al.,* 2011
Zea mays L.	Increased enzyme activities of Superoxide dismutase (SOD), Catalase (CAT), Ascorbate peroxidase (APX), Guaiacol peroxidase	Javadmanesh *et al.,* 2012
Vigna mungo (L.) Hepper	Increases the contents of anthocyanin, flavonoids and soluble phenols	Shaukat *et al.,* 2013
Vigna mungo (L.) Hepper	Increased enzyme activities of Superoxide dismutase (SOD), Catalase (CAT), Ascorbate peroxidase (APX), Glutathione peroxidase (GPX)	Dwivedi *et al.,* 2015
Vigna aconitifolia (Jacq.) Maréchal	Increased enzyme activities of Superoxide dismutase (SOD), Catalase (CAT), Ascorbate peroxidase (APX), Glutathione peroxidase (GPX)	Dwivedi *et al.,* 2015
Zea mays L.	Enhanced anthocyanin; increased enzyme activities of Catalase (CAT), Ascorbate peroxidase (APX) and Glutathione S-transferase (GST)	Rudnóy *et al.,* 2015
Oryza sativa L.	Enhanced activities of enzymes such as Superoxide dismutase (SOD), Catalase (CAT) and Peroxidase (POX)	Inostroza-Blancheteau *et al.,* 2016
Oryza sativa L.	Priming imprints observed and induction of cross-tolerance	Thomas *et al.,* 2020
Oryza sativa L.	Increased Phenylalanine ammonia lyase (PAL) activity, flavonoids content, anthocyanin and epicuticular wax content	Thomas and Puthur, 2020

strongly and quickly against the abiotic stress, along with enhanced plant growth and better yield (Jisha *et al.,* 2013).

Priming of plants at seedling stage is comparatively unconventional but has been proved to be sometimes equally beneficial to the plant (Capanoglu, 2010). UV-B priming at seedling stage has been carried out in many different crops such as *V. mungo* and *V. aconitifolia* (Dwivedi *et al.,* 2015), *V. unguiculata* (Mishra *et al.,* 2008) and *Momordica charantia* (Mishra *et al.,* 2009). In all these studies, increased production of plant pigments and metabolites like ascorbic acid, glutathione, tocopherol etc. accompanied with positive impact on plant morphology have been observed.

Significance of UV-B Priming

Morphological Changes : Priming of crops with UV-B radiation has shown promising results in terms of enhanced growth and biomass accumulation in several studies till now (Yao *et al.,* 2007; Kacharava *et al.,* 2009 and Behn *et al.,* 2010). Several researches have shown positive influence of UV-B priming on crops with respect to the increased rate of seed germination (Shaukat *et al.,* 2013). Vegetative growth enhanced along with other observations like increase in root and shoot length, increased leaf area in some crops (Wargent and Jordan, 2013), while reduced leaf size but increased thickness of leaf (Bornman and Vogelmann, 1991; Staxen & Bornman, 1994 and Rozema *et al.,* 1997) or increased leaf mass per unit area in some plants (Sprtova *et al.,* 2003 and Laposi *et al.,* 2009), increase of leaf epidermal waxes (Cen and Bornman, 1993) and reduction in leaf number as noticed in *Cucumis sativus* and *Lactuca sativa* (Krizek *et al.,* 1998). In some UV-B primed crops, higher yield, increased pod biomass and increased flower production were observed. In peppermint, integrated treatment of UV-B and Photosynthetically Active Radiation (PAR) had resulted in development of higher number of peltate glandular trichomes per leaf (Behn *et al.,* 2010).

Physiological Changes : UV-B radiation in general promotes the crop production, nutritional quality, stress

TABLE 2

Different morphological changes generally observed in plants on UV-B priming

Plant characteristics	Change observed	References
Vegetative growth	Increase	Wargent and Jordan, 2013
Biomass accumulation	Increase	Yao *et al.,* 2007; Kacharava *et al.,* 2009; Behn *et al.,* 2010
Root length	Increase	Wargent and Jordan, 2013
Shoot length	Increase	Wargent and Jordan, 2013
Seed germination rate	Increase	Shaukat *et al.,* 2013
Flower production	Increase	Thomas and Puthur, 2017
No. of peltate glandular trichomes per leaf	Increase	Behn *et al.,* 2010
Pod biomass	Increase	Thomas and Puthur, 2017
Crop yield	Increase	Thomas and Puthur, 2017
Leaf area	Increase	Wargent and Jordan, 2013
Leaf size	Decrease	Ravindran *et al.,* 2010
Leaf thickness	Increase	Bornman and Vogelmann, 1991
Leaf mass per unit area	Increase	Šprtová *et al.,* 2003; Láposi *et al.,* 2009
Accretion of leaf epidermal waxes	Increase	Cen and Bornman, 1993
Leaf number	Decrease	Krizek *et al.,* 1998
Fruit size	Increase	Loconsole and Santamaria, 2021

tolerance and plant defense against pests and herbivores (Demkura *et al.,* 2010; Austin & Wilcox, 2012; Ballare *et al.,* 2012; Suklje *et al.,* 2014; Williamson *et al.,* 2014 and Garcia-Cela *et al.,* 2015). Physiologically we observe higher accumulation of various secondary metabolites, increased hormonal activity, increased photosynthetic pigments content and increased antioxidative activity of the plant. Exposure to UV-B upregulates the genes responsible for pathogenesis in plants, hence protecting them against pests and pathogens (Ballare *et al.,* 2012). Increase in hormonal activity like jasmonic acid provides protection against herbivory (Song *et al.,* 2015). Increased accumulation of secondary metabolites enhances the nutritional and medicinal quality of the plant (Schreiner *et al.,* 2012). UV-B exposure made plants robust and also increased growth rate of trees in Eastern New Zealand and led to agricultural expansion in South Eastern South America (Andrady *et al.,* 2015).

Contents of plant pigments like chlorophyll, carotenoids and anthocyanins are enhanced under UV-B stress (Xu & Qiu, 2007; Mishra *et al.,* 2008; Kacharava *et al.,* 2009; Shaukat *et al.,* 2013; Badridze *et al.,* 2015; Rudnoy *et al.,* 2015 and Badridze *et al.,* 2016). Increased production of carotenoids protects the plant from oxidative damage caused due to abiotic stress (Jaleel *et al.,* 2009). The combined use of ambient UV-B (0.6 Wm^{-2}) and Photosynthetically Active Radiation (PAR) enhanced the production of essential oil and total monoterpene in *Mentha piperita* (Behn *et al.,* 2010). Several primary metabolites like proteins, total sugar and total amino acid content are accumulated more in UV-B primed plants (Zu *et al.,* 2004; Kacharava *et al.,* 2009; Kosova *et al.,* 2011; Badridze *et al.,* 2015 and Badridze *et al.,* 2016). Significant increase in total grain nitrogen content and grain storage protein (glutelin) in UV-B primed rice plants was observed (Hidema *et al.,* 2005). Also significant increased amylose concentration was observed in UV-B irradiated rice plants (Xu and Qiu, 2007).

Antioxidants : Different abiotic stresses result in increased activities of enzymatic antioxidants like

TABLE 3

Different physiological changes generally observed in plants on UV-B priming

Plant characteristics	Change observed	References
Nutritional quality	Increase	Schreiner *et al.,* 2012
Stress tolerance	Increase	Thomas *et al.,* 2020
Plant defense against pests and herbivores	Increase	Meyer *et al.,* 2021
Accumulation of secondary metabolites	Increase	Thomas and Puthur, 2020
Chlorophyll content	Increase	Thomas and Puthur, 2017
Carotenoid content	Increase	Thomas and Puthur, 2017
Anthocyanin content	Increase	Thomas and Puthur, 2017
Activity of genes responsible for pathogenesis	Increase	Ballaré *et al.,* 2012
Antioxidant activity	Increase	Thomas *et al.,* 2020
Jasmonic acid biosynthesis	Increase	Song *et al.,* 2015
Total sugar content	Increase	Sen *et al.,* 2021
Total amino acid content	Increase	Sen *et al.,* 2021
Total grain nitrogen content	Increase	Hidema *et al.,* 2005
Grain storage protein (glutelin) content	Increase	Hidema *et al.,* 2005
Grain amylose concentration	Increase	Xu and Qiu, 2007
Phenol content	Increase	Rudnóy *et al.,* 2015

Superoxide Dismutase (SOD), Catalase (CAT), Peroxidase, Glutathione reductase and accumulation of non-enzymatic antioxidants like ascorbic acid, a-tocopherol, glutathione, proline that are involved in free radicals scavenging (Takeuchi *et al.,* 1996; Olsson *et al.,* 1998; Yanqun *et al.,* 2003; Mishra *et al.,* 2009; Gill & Tuteja, 2010; Miller *et al.,* 2010; Javadmanesh *et al.,* 2012; Hideg *et al.,* 2013; Shaukat *et al.,* 2013; Aboul Fotouh *et al.,* 2014; Das and Roychoudhury, 2014; Andrady *et al.,* 2015; Dwivedi *et al.,* 2015; El-Shora *et al.,* 2015; Badridze *et al.,* 2016 and Inostroza-Blancheteau *et al.,* 2016). UV-B priming may regulate different metabolic pathways and antioxidants like glutathione pathway, phenylpropanoids, cinnamates, flavonoid pathways and pyridoxine biosynthesis pathways (Hideg *et al.,* 2013). Exposure to UV radiation increases the incorporation of newly assimilated carbon to flavonoids suggesting an energy shift in order to tolerate the stress (Guidi *et al.,* 2011; Ballare *et al.,* 2012). Priming using UV-B radiation has also shown to increase Vitamin C and E contents in kidney beans and sugar beet (Ouhibi *et al.,* 2014). The low levels of UV radiation stimulated the antioxidants production and thereby enhanced the nutritional quality of agricultural crops. This also resulted in increased tolerance of these crops towards various environmental factors (Teklemariam and Blake, 2003; Kacharava *et al.,* 2009; Aboul Fotouh *et al.,* 2014 and Thomas & Puthur, 2017). The UV-B exposed maize plants showed enhanced phenol content and enhanced activities of CAT, APX and glutathione S transferase (GST) (Rudnoy *et al.,* 2015).

Research Insights

The development of tools and procedures that permit for the estimation of pragmatic UV radiation exposures of discrete plants, natural ecosystems and agricultural contexts need further attention. In models that examine the combined impacts of alterations in UV radiation, temperature and vegetation on terrestrial ecosystems, spectral sensitivities and UV radiation exposures are required. The myriad technical challenges involved in conducting UV radiation studies, on the other hand, might be scary to researchers who are just getting started in this field. Aphalo *et al.* (2012) provide a complete guide

TABLE 4

Changes in antioxidants generally observed in plants on UV-B priming

Plant characteristics	Change observed	References
Activity of enzymatic antioxidants	Increase	Thomas and Puthur, 2020
Superoxide Dismutase (SOD) activity	Increase	Sen and Puthur, 2020
Catalase (CAT) activity	Increase	Sen and Puthur, 2020
Glutathione reductase (GR) activity	Increase	Rudnóy *et al.,* 2015
Glutathione S Transferase (GST) activity	Increase	Rudnóy *et al.,* 2015
Ascorbate Peroxidase (APX) activity	Increase	Rudnóy *et al.,* 2015
Peroxidase activity	Increase	Thomas and Puthur, 2020
Phenylpropanoids biosynthesis	Increase	Hideg *et al.,* 2013
Cinnamates biosynthesis	Increase	Hideg *et al.,* 2013
Flavonoid biosynthesis	Increase	Hideg *et al.,* 2013
Pyridoxine biosynthesis	Increase	Hideg *et al.,* 2013
Glutathione biosynthesis	Increase	Hideg *et al.,* 2013
Vitamin C content	Increase	Ouhibi *et al.,* 2014
Vitamin A content	Increase	Ouhibi *et al.,* 2014
Incorporation of newly assimilated carbon to flavonoids	Increase	Guidi *et al.,* 2011; Ballaré *et al.,* 2012

to all areas of experiment plan, execution, analysis, and instrumentation, which will assist standardize protocols and assure accurate, relevant findings.

Experiments on the effects of UV light need precise monitoring of UV radiation. Double-grating spectroradiometers are ideal for these measurements because they reduce 'stray light' in the instrument and refine the signal provided to the detector. But, diode-array spectroradiometers are supplementing the mechanical double-grating spectroradio meters due to being more efficient and cost-effective, though eliminating 'stray light' is still a problem in these. When taking measurements in the field, the instruments' sensitivity to temperature is also a concern. It is feasible to design corrections algorithms for specific units in some circumstances (*e.g.,* Baczynska *et al.,* 2011), but one must evaluate if differential heating of the unit under direct bright sunlight can be effectively mimicked in a test chamber. In situations with significant geographical variability in UV irradiance, several ecological investigations need measurements of time-integrated biologically effective (UV_{BE}) UV radiation (for example, within the bounds of plant canopies, soil surfaces below plant canopies, etc.). Parisi *et al.* (2010) employed UV dosimeters to describe the UV-radiated environment of discrete leaves in plant canopies, as well as to assess minute variations in plants exposed to UV radiation in heterogeneous environments. These dosimeters may have special use for long-term monitoring of incident UV radiation on standing crop if they are calibrated against spectroradiometers on field.

Ballare *et al.* (2011) explored methodological challenges in supplemental UV radiation experiments when filtered fluorescent UV lamps don't have a spectral output that completely equates to the sun spectrum. A novel filter, known as the urate anion liquid filter, has been created that allows fluorescent UV lights to more nearly resemble sunshine (Sampath-Wiley and Jahnke, 2011). This novel filter blocks more shortwave UV-B light (305 nm) while transmitting more longwave UV-B (310 nm) than typical cellulose diacetate filters.

Future studies should be targeted not only on the activities showing greater changes but also on the minor variations that are deemed insignificant in conclusion of a research, like change in leaf orientation, shape and colour, small changes in the concentrations of different biochemicals etc. Indirect impacts of UV exposure are typically more prominent than direct effects and they must be considered in order to gain a comprehensive understanding of UV radiation's role as a regulator and modulator of ecosystem and organism response. Global climatic changes, such as increased CO_2 and greater temperatures, will almost certainly be overlaid on the predicted growth in UV-B radiation in the future decades. As a result, if plant breeders/farmers are to choose crop varieties that have better adaptation to tolerate these stressors, and ecologists are to forecast the expected effects for natural ecosystems, investigations of the combined effects of environmental variables and UV-B radiation will be required. Other climatic variables and their inter connections, as well as their consequences on plants and communities, should be considered when analyzing the effects of stress. UV-B radiation exposure is affected not just by variations in ozone levels, but also through alterations in land use and climatic events such as predicted fluctuations in rainfall, variations in cloud cover in different places, and snow and ice melting. The occurrences are anticipated to have an impact on ecosystem functioning and food production, necessitating a comprehensive study strategy that considers the effect of UV radiation in a constantly changing environment. Evidence is mounting that these inter-connected elements of UV radiation, alterations in ozone, temperature and environment are affecting plant and ecosystem responses, according to study thus far. More research into where possible favourable impact tipping points are happening will improve our understanding and capacity to forecast potential future impact from interactions between UV radiation and other concurrent environmental challenges. For future plant response estimates, an integrated research method under realistic conditions is required.

A greater knowledge of UV-B priming mechanisms will aid in the development of seed production technologies as well as the development of a 'priming reagent' that can imitate the effects of priming to increase crop stress tolerance. Furthermore, the key stages and degree of priming application for subsequent important stages and applications should be improved, as this may be species specific. The role of *UVR8* in nucleoplasmic gene transcription, the nature of COP1 signaling in the *UVR8* pathway and the link between *UVR8* activation and repression of hormone production or signaling are all questions that need to be explored further. Further research in these areas should help us better understand the *UVR8* UV-B signaling pathway and how UV-B interacts with other environmental elements.

High UV-B distress appears to be required for ROS-mediated signaling. This finding raises two key research questions for the future. To begin, it is necessary to determine the specific mix of ambient variables and physiological acclimation stages that will result in either eustress or distress. Second, how plants 'Balance' general ROS-specific signaling pathways with stimuli-specific systems such as UV-B photoreceptor-mediated responses is a fascinating follow-up question. Understanding the basic issues underlying one of the most important plant characteristics, the ability to adapt to changing environmental conditions, should be investigated thoroughly.

The current study shows that priming seeds and seedlings with mild dose of UV-B can improve plant responses to following stress, particularly salt stress and that UV-B priming can produce cross-tolerance, enhancing rice potential to adapt to other kinds of environmental stresses. The study also shows that priming effects may be seen in seedlings developed from primed seeds, indicating that priming imprints exist.

The need for improved prediction of good and negative agricultural consequences of UV photomorphogenesis is critical and with global variations in UV-B fluxes expected to remain unpredictable for the rest of this century, UV radiation will continue to be a key environmental impact. Complementing agriculture systems with the selection of cultivars or lines which may respond well to the local UV environment, as well as the advancement of over expression or silencing tools for key UV-B signaling components, is arguably critical in monopolizing the UV response for desired end points in a changing climate.

For decades research studies had described only the harmful impact of UV radiation on plants, which is justifiable since these experiments used unbalanced spectral manipulations and unpractically high UV doses. Some recent research works acknowledged the beneficial aspects of UV-B exposure on plants after employing realistic, balanced, monochromatic UV-B fluxes. UV priming of seeds and seedlings is an eco-friendly, effective, convenient and inexpensive method for preparing plants for unfavourable, high UV exposure in future. Apart from providing stress tolerance towards UV, it also seemed to provide tolerance towards other abiotic and biotic stresses. It is a very promising strategy for enhancing the quality of crop plants and elevating the agronomic gain overall. Exposing plants to low doses of UV-B escalates the production of the antioxidants, phenolics, pigments and enzymes, overall strengthening defense system and increasing photosystem competency of the plant. There is a need of an extensive research on the impact of UV-B priming at molecular level in plants. Since UV radiation has been proved to regulate signal transduction activities in photosynthetic cells, it is highly recommended to investigate more into the link of these signaling episodes with the process of adaptation and acclimation in plants after UV exposure. The function of UV light in signal transduction processes in photosynthetic cells must be investigated thoroughly. Exploring the link between these signaling events and the adaptation and acclimation processes that occur under UV exposure is critical. Furthermore, a thorough knowledge of the *UVR8*-mediated UV-B signaling pathway may aid in reducing undesirable consequences or maximizing the beneficial effects of UV-B exposure in agricultural crops to increase quality and production. Comprehension of the interaction between UV-B and signaling biomolecules and comparative study of photomorphogenic responses to responses to other abiotic and biotic stresses, *UVR8*-mediated UV-B signaling may become a convenient tool to manipulate the growth of a plant and its tolerance to these environmental stresses. Having a deeper knowledge of the mechanism of UV-B priming will provide opportunities at improving plant quality and stress tolerance and enhancing the crop productivity and yield.

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