Plant Responses: UV-B Avoidance Strategies

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Abstract

Solar radiation is the major source of energy in the universe and critical for the plant growth and development. The UV-B radiations, the small fraction of solar radiation affect the plant growth via altering various morphological, physiological, and molecular responses. However, plants cope UV-B stress using their defense system which is not strong enough to recover the damage and yield losses caused by enhanced or ambient UV-B exposure. Hence, various strategies have been developed by plant scientists in the past years to circumvent or mitigate the UV-B stress. In the present chapter, we have discussed the impact of UV-B stress upon overall performance of plants including yield. In addition, various available UV-B-avoiding strategies have been addressed such as exclusion of solar UV-B by UV-B cutoff filters and seed priming with magnetic field which are useful to provide UV-B stress tolerance to the plants.

Keywords

UV-B exclusion · Growth · Photosynthesis · UV-B · Magneto-priming · Crop yield

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7.1 Introduction

The solar radiation affects all living organisms on the earth directly or indirectly, and it is the major source of energy essential for the growth and development of the plants. In general, solar radiation reaches to the Earth surface is mainly composed of ultraviolet (UV), visible, and infrared rays. Among these rays, particularly, UV radiations are composed of three types of wavelengths: UV-A (315–400 nm), UV-B (280–315 nm), and UV-C (200–280 nm). The UV-B radiation constitutes a small fraction of total solar radiation which reaches to the Earth's surface due to stratospheric ozone depletion (Kataria et al. 2014a, b; Bornman et al. 2019) and it is currently reached to its maximum level which is a serious concern to the world. Towards controlling the ozone depletion, Montreal protocol (an international agreement to protect ozone depletion) suggested that ozone layer can be revert to the pre-1980 levels at the mid-latitudes by 2040–2070, if it is followed properly by participating countries (Mohammed and Tarpley 2010; Bais et al. 2018, 2019). However, the rise in the levels of greenhouse gases could delay this return (Newman et al. 2001; Bais et al. 2019). UV-B radiation plays an imperative role in terrestrial ecosystems but, it can represent a risk for plants in excess. The excess UV-B exposure induces various negative effects to which plants can respond with defense and adaptive mechanisms (Kataria et al. 2014a; Rácz et al. 2018). Photoexcitation of biomolecules like nucleic acids, proteins and lipids via absorbing UV-B can cause alteration in the various biological processes (Caldwell et al. 2007; Jenkins 2009; Tian and Yu 2009; Kataria et al. 2014a). The UV-B exposure is known to delay seedling emergence, reduce leaf area, leaf length, leaf thickness and midrib thickness. Furthermore, curling of cotyledons/leaves, bronzing/glazing of leaves, leaf chlorosis with necrosis, reduced internode length with overall plant height, and delayed flowering are the symptoms shown by various crop plants (Caldwell et al. 1995, 2007; Robson et al. 2015; Suchar and Robberecht 2015). It has been suggested that these variety of symptoms are the result of perturbed hormone metabolism and cell wall loosening due to UV-B rays (Hectors et al. 2007; Casati and Walbot 2003). In spite of morphological changes, physiological parameters are also known to be affected via UV-B exposure. The photosynthetic machinery of plants is very sensitive to excess UV-B exposure which leads to hamper the carbon, nitrogen metabolism, photosynthetic efficiency and ultimately reduces the biomass accumulation and crop yield (Kataria et al. 2013, 2014a; Dotto and Casati 2017). Earlier, various indoor studies have shown that UV-B exposure can impair three major processes of photosynthesis: CO_2 fixation, photophosphorylation, and stomatal movement to regulate the CO_2 supply (Allen et al. 1998; Teramura and Sullivan 1994; Kataria et al. 2014a). The prolonged exposure of UV-B rays destruct the carotenoids and chlorophyll which ultimately reduces the photosynthetic performance of plants (Nogues and Baker 1995; Baker et al. 1997; Allen et al. 1998; Wilson et al. 1995; Yu et al. 2013). It has been reported that photosystem-II (PS-II) is very sensitive to UV-B exposure due to their chemical organization of D1 and D2 proteins along with oxygen-evolving complex (Kataria et al. 2014a, b; Faseela and Puthur 2018; Schultze and Bilger 2019; Çiçek et al. 2020). The chlorophyll *a* (chl *a*) fluorescence parameters such as polyphasic fluorescence transients (OJIP transients) show lower fluorescence yield particularly at I to P-phase in leaves of plants grown under UV-B stress (Kalaji et al. 2018; Kataria et al. 2020a, 2021).

In addition, prolonged exposure of UV-B rays triggers oxidative stress due to increased production of reactive oxygen species (ROS) in plants (Jain et al. 2004; Kataria et al. 2017a, b). However, increased ROS production can be neutralized through enzymatic and non-enzymatic defense mechanisms (Jain et al. 2004; Kataria et al. 2007; Dias et al. 2020). The enzymatic defense system includes antioxidant enzymes like superoxide dismutase (SOD), catalase (CAT), and enzymes of Halliwell/Asada pathway, whereas non-enzymatic defense system includes molecules like ascorbate, tocopherol, glutathione, carotenoids, and phenolics (Jain et al. 2004; Hideg et al. 2013; Kataria et al. 2007; Dias et al. 2020). Although plants have evolved with these defense systems, these are not enough to recover the damage and yield loss caused by prolonged UV-B exposure. In this scenario, UV-B rays reaching on the Earth could not be avoided and so it becomes crucial to find out the ways which can protect the plants from the UV-B exposure. However, various methods are available to avoid or mitigate UV-B stress, but exclusion of solar UV component from natural solar radiation and magneto-priming is most commonly used methods found in the literatures (Krizek and Mirecki 2004; Kataria et al. 2013, 2017a, 2020a, 2021; Prajapati et al. 2020; Raipuria et al. 2021). Therefore, present chapter is aimed to provide an overview about avoiding strategies used to improve the plant tolerance towards UV-B stress by circumvent the harmful effects of UV-B radiations.

7.2 Solar UV Exclusion as a Strategy to Avoid the Effects of UV-B Stress

It is difficult to get the place devoid of UV-B rays, therefore, UV-B stress related studies were conducted under growth chambers and green houses equipped with UV-B lamps. Later by 1990s, the scientific community questioned the usage of this strategy, as UV-B lamps could not provide the natural ratios of UV-B/UV-A and UV-B/PAR radiations (Caldwell and Flint 1994, 1997; Krizek and Mirecki 2004). Further, it was suggested that outdoor studies should be carried out under ambient solar radiations to evaluate the actual impact of solar UV-B radiation on the plant growth and development. Now, there are two widely preferred ways of conducting outdoor studies aiming to see the effect of UV-B exposure: (1) UV-B enhancement and (2) UV-B attenuation approach (Rousseaux et al. 2004). In UV-B enhancement approach, solar radiations are supplemented with UV-B lamps to mimic the condition of increased UV-B incidence due to ozone depletion. On the other hand, UV-B attenuation is performed using solar UV-B exclusion filters to mimic the (–UV-B) conditions (Lingakumar et al. 1999; Phoenix et al. 2000; Krizek and Chalker 2005; Zhang et al. 2014; Kataria et al. 2013, 2014b; Kataria and Guruprasad 2012a, b, 2014, 2015). The plastic screens or polyester filters can reduce the ambient UV-B levels and can be used to provide the sub-ambient and nearambient UV-B treatment conditions. These two outdoor approaches are simple, reliable, and cost-effective which can be used to see the actual impact of ambient or enhanced UV-B on the plants performance.

7.2.1 Plant Growth, Photosynthesis, Antioxidant Defense, and Yield Under Solar UV-B Exclusion

In the natural environment, plants are exposed to combined stresses which in turn cause several changes in gene expression, plant metabolism, and morphology. Enhancing the crop productivity under variable climate has been a major challenge to the entire agricultural scientific community. One of the unavoidable stresses, UV-B radiations, hamper the plant growth and development by damaging the cell membranes, DNA, RNA, cell organelles like mitochondria, chloroplasts, etc. (Hollosy 2002; Jain et al. 2003, 2004; Kataria et al. 2014a; Vanhaelewyn et al. 2020). However, the extent of damage depends on the intensity with duration of UV-B irradiance and most importantly the plant developmental stage getting exposed. In regard to overcoming UV-B stress, ambient UV-B exclusion is a potential strategy to obtain higher growth and biomass/yield. Several reports have revealed that plants grown under solar UV-B exclusion conditions showed increased growth in both aboveground and belowground parts of the plants. For example, various plant species like radish, barley, mung bean, pea, pumpkin, soybean, Cyamopsis, Vigna, wheat, cucumber, cotton, sorghum, amaranthus, and trigonella showed increased growth in terms of plant height, leaf area, specific leaf weight, leaf weight ratio, overall biomass accumulation, efficiency of PSII, photosynthesis, and yield under solar UV-B exclusion conditions (Pal et al. 1997; Mazza et al. 1999; Zavalla and Botto 2002; Krizek and Mirecki 2004; Amudha et al. 2005; Guruprasad et al. 2007; Pal et al. 2006; Kanungo et al. 2013; Kataria and Guruprasad 2012a, b, 2014, 2015; Kataria et al. 2013; Sharma et al. 2019). Similarly, ambient UV-B exclusion allowed plants to produce more tillers and branches in monocots and dicots, respectively (Mazza et al. 1999; Coleman and Day 2004; Kataria and Guruprasad 2012a). In *Vaccinium uliginosum*, it was reported that ambient UV-B exclusion increases the biomass of belowground tissues (Rinnan et al. 2005). The UV-B-free environment improved the photosynthetic capacity up to 33% over normal condition grown common beans plant which suggested that UV-B rays primarily reduces the photosynthetic rate and CO_2 fixation (Moussa and Khodary 2008). A number of reports have shown the enhanced net photosynthetic rate and stomatal conductance upon UV-B exclusion in Populus (Schumaker et al. 1997), maize, and mung bean (Pal et al. 1997), wheat and pea (Pal et al. 2006), *Vaccinium uliginosum* (Albert et al. 2008), sorghum (Kataria and Guruprasad 2012b), *Amaranthus tricolor* (Kataria and Guruprasad 2014), and wheat (Kataria and Guruprasad 2015). In another reports, it was shown that the UV-B exclusion via polyester filters increased the root biomass, number of nodules, and nodule fresh weight along with increased nitrogenase activity (by 120%) and leghemoglobin content (by 63%) in fenugreek (Sharma and Guruprasad 2012). Other reports showed the higher levels of α-tocopherol in UV-B-excluded plants which are important for translocation of photosynthates from leaves to root (Chouhan et al. 2008; Baroniya et al. 2014; Kataria et al. 2014b). Secondary metabolites are the byproducts of various metabolic pathways which are known to help the plants in the adaptation to its surrounding climate (Alvarez 2014). The saponins are the triterpene glycosides known to have antimicrobial, antitermitic properties, and their concentration in the plants increased under higher light intensities (Mathur et al. 2000; Maulidiani et al. 2012). In cotton, UV-B-excluded plants showed increased plant height due to increased number of elongated nodes. These increased elongated nodes showed the lower amount of saponins as compared to plants grown under ambient UV-B conditions. This study proved that saponins act as growth inhibitor in ambient UV-B conditions (Dehariya et al. 2018).

The plants grown under solar UV-B exclusion conditions showed enhanced photosynthetic performance due to higher photosynthetic pigments, efficiency of PSII, electron transport rate, photosynthetic rate, and stomatal conductance with increased activity of photosynthetic enzymes such as carbonic anhydrase (CA), Ribulose-1,5 bisphosphate carboxylase/oxygenase (Rubisco), and phosphoenolpyruvate carboxylase (PEPC) over the plants grown under ambient solar UV-B conditions (Solanki et al. 2006; Kataria et al. 2013, 2014a; Kataria and Guruprasad 2012b, 2014, 2015). In a recent study, UV-B exposed scot pine seedlings showed decreased quantum yields and electron transport at both donor and acceptor sides of photosystems and the performance indexes (Çiçek et al. 2020). However, chlorophyll fluorescence parameters such as quantum efficiencies, phenomenological fluxes, and performance indices were enhanced by UV-B exclusion which suggests the adverse impact of ambient UV-B on these parameters (Kataria et al. 2013; Kataria and Guruprasad 2014, 2015). On the other side, solar UV-B exclusion has been observed to significantly increase the RuBisco activity and protein in the in microalgae and higher plants; it indicates that the ambient or enhanced UV-B lowers the Rubisco activity and protein content (Bischof et al. 2000, 2002; Pedro et al. 2009). The reduced activity of Rubisco could be due to suppression of genes encoding subunits of Rubisco and damage from the ROS generated under UV-B radiations (Jordan et al. 1992; Mackerness et al. 1999; Dehariya et al. 2012; Shine and Guruprasad 2012a, b; Kataria et al. 2013).

The soluble sugars, polysaccharides, secondary metabolite, and total flavonoid contents were also increased in the medicinal plant *Prunella vulgaris* upon UV-B exclusion (Chen et al. 2019). In another report, cumulative impact of altitude, cultivar, and solar radiation on the growth, physiology, and yield was analyzed. The exclusion of UV-B rays from solar radiation prompted the photosynthetic rate, stomatal number, and conductance with dry matter of Boloso-1 cultivar of *Colocasia esculenta* (L.) species (Derebe et al. 2019). In a recent report, UV-B exposed plants of *Silene littorea* showed increased concentration of anthocyanin (20–30%) and UV-B-absorbing compounds (12–25%) over UV-B-excluded plants which gave a clue of their involvement in photoprotection (Del Valle et al. 2020).

Overall solar UV-B exclusion can alter various morphological and physiological parameters leading to the improved plant performance (Fig. 7.1). For instance, UV-B

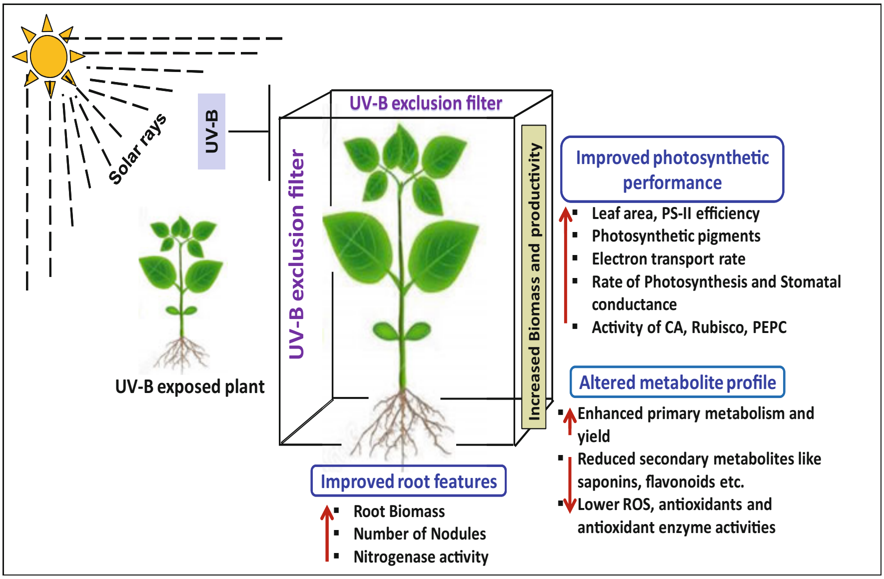

Fig. 7.1 The impact of solar UV-B exclusion upon various parameters determining overall performance the plants

exclusion increases photosynthesis, reduces the content of UV-B-absorbing substances, ROS and antioxidants (ascorbic acid and α-tocopherol); and lower activities of antioxidant enzymes such as SOD, peroxidase (POD), ascorbic acid peroxidase (APX), and glutatione reductase (GR) (Baroniya et al. 2013; Dehariya et al. 2011, 2012; Kataria et al. 2013, Kataria and Guruprasad 2012a, b, 2014, 2015; Sharma et al. 2019). Also, several others reports claim that solar UV-B exclusion improve the metabolism pattern that leads to enhanced primary metabolism and reduced synthesis of secondary products, like saponins, flavonoids, and phenolics compounds (Alemu and Gebre 2020; Dehariya et al. 2018; Kataria et al. 2013, 2014b).

The crop productivity depends on the overall performance of plants grown in the field under dynamic climate. The plant performance is proportionally related to yield and may vary due to their environmental interaction. The incidence of damaging effects caused by UV-B exposure varies according to the locations around the globe (Teramura et al. 1990). Several research groups have suggested that impact of UV-B radiation is high in tropical regions including India due to longer exposure of sunlight (Agrawal and Rathore 2007; Amudha et al. 2005; Guruprasad et al. 2007; Kataria and Guruprasad 2012a, b, 2014, 2015). Therefore, ambient solar UV-B radiation causes significant yield loss on terrestrial plants of tropical regions (Kataria et al. 2013; Kataria and Guruprasad 2014; Zhu and Yang 2015). Primarily, enhanced UV-B exposure alters the leaf ultrastructure and damages the photosynthetic apparatus, PS-II efficiency, and hence affects the net photosynthesis and ultimately reduces the yield of plants (Kakani et al. 2003; Kataria et al. 2014a). There are several reports which have been proved to enhance the yield in various crops. In pumpkin (*Cucurbita pepo* L.), the UV-B filtration from solar radiation doubled the yield (Germ et al. 2005). In a field study, the effect of UV-A/UV-B exclusion showed up to 50% increased yield of *Cyamopsis tetragonoloba* among three tested tropical legumes (Amudha et al. 2005). In another greenhouse study conducted by using UV absorbing films showed that UV-B exclusion enhanced the fruit size and yield by 20% in eggplant (Kittas et al. 2006). Similarly, two strawberry cultivars named Camarosa and Ventana showed enhanced productivity of 30% and 20%, respectively, when grown in the absence of UV radiation (Casal et al. 2009); however, the ripening of fruits was delayed and no nutritional parameters were improved in both cultivars. In a field study, four different varieties of wheat (Purna, Vidisha, Naveen Chandausi, and Swarna) grown under UV-B cutoff filters showed the significant enhancement in grain yield (44%) of wheat variety of Purna; Vidisha showed 65% increase after the exclusion of UV-B. However, other two varieties Swarna and N. Chandausi did not showed significant enhancement (Kataria and Guruprasad 2015). The solar UV-A + UV-B and UV-B exclusion showed enhanced yield parameters in terms of weight of total bolls and fibers (cotton), fresh weight of leaves (amaranthus), number of ears/panicles, grain yield per plant (wheat and sorghum), and number of seeds and seed weight (soybean) (Baroniya et al. 2011, 2014;Kataria and Guruprasad 2014, 2015; Kataria et al. 2013, 2014b). However, the extent of improved yield parameters was more in UV-B exclusion rather than UV-A + UV-B exclusion (Kataria et al. 2013). In *Curcuma longa*, UV-B exclusion grown plants showed significant increment in the photosynthetic rate, biomass accumulation, curcuminoid, and curcumin yield (Ferreira et al. 2016). To check the performance of monocots and dicots under ambient UV-B stress, Kataria et al. (2013) and Kataria and Guruprasad (2012a, b, 2014, 2015) research group conducted a comparative study and concluded that UV-B stress in the tropical environment lowers the PS-II efficiency, assimilation of nitrogen and carbon dioxide, which ultimately leads to reduced plant growth and productivity. They also showed that dicots are more sensitive than monocots for UV-B radiations. In addition, several reports have witnessed the improved crop yield under solar UV-B exclusion conditions when compared with ambient UV-B stressed conditions (Guruprasad et al. 2007; Kataria and Guruprasad 2012a, b; Roro et al. 2016; Sharma et al. 2019). On the basis of discussed literatures, solar UV-B rays considerably hamper the plant growth, development, and productivity, and if ozone depletion continues, it will allow more UV-B rays reaching to the Earth's surface which will further have more biological sequences to the plant growth and development.

7.3 Magneto-priming as a Strategy to Avoid UV-B Stress

Magneto-priming is a method of seed priming, where dry seeds are treated with magnetic field (MF). For improved performance of seeds, exposure timing and intensity of MF always need to be optimized according to the species (Sarraf et al. 2020, 2021). For example, the treatment of soybean seeds with static magnetic field (SMF) strength of 200 mT for 1 h has been used to improve its performance and for the alleviation of adverse effects caused by ambient or supplemental UV-B stress (Fatima et al. 2021b; Kataria et al. 2017a, 2020a, 2021; Raipuria et al. 2021). In last decade, several scientific reports have been published showing magneto-priming based improved seed germination, seed vigor, seedling emergence, seedling growth, increased biomass accumulation, photosynthesis, and yield (Shine et al. 2011, 2012; Bhardwaj et al. 2012; Sarraf et al. 2020, 2021). Besides improved seed performance, magneto-priming of seeds have been shown to provide the tolerance against various abiotic stresses such as drought, salinity, heavy metal, and UV-B stress during seed germination and subsequent developmental stages of plants (Anand et al. 2012; Fatima et al. 2021a, b; Baghel et al. 2016, 2018, 2019; Kataria et al. 2015, 2017a, b, 2019, 2020a, b; Raipuria et al. 2021; Sarraf et al. 2020, 2021).

These improved performances of seeds after magneto-priming raise the question that how does SMF interacts with biological systems and improves their growth and performance. The answer of this question lies in the magneto-reception theory which accounts for the reaction of plants to DC/static fields and alternating magnetic fields (Camps-Raga et al. 2009; Shine et al. 2011; Shine and Guruprasad 2012a, b). As per this theory, there are two mechanisms named as ion cyclotron-resonance (ICR) and radical pair model to understand the influence of magneto-priming on plants (Galland and Pazur 2005; Fatima et al. 2021b). As per radical pair model, the biochemical reaction involving spin-correlated radical pairs should be sensitive to external magnetic fields. The biological reaction involving the spin selectivity and thus the sensitivity to magnetic field are the emission intensity of the photosynthetic reaction center and the triplet yield. As evidenced from the experimental and theoretical studies, the application of magnetic fields increases the radical lifetime and average radical concentration and shoot up the probability of radical reactions with the cellular components. These examinations apply also to the enzymatic systems entailing the radical pair formation and recombination (Galland and Pazur 2005). The external magnetic field can also modulate the emission intensity and the radical pair intermediates and triplet yields that occur in photosystems I and II of green plants. The increased water uptake in SMF-treated seeds as compared to untreated seeds is explained by the assumption that the magnetic field interacts with ionic currents in the cell membrane of the plant embryo (García-Reina and Arza-Pascual 2001).

When the magnetic field is applied, the chemical reaction rates modulate according to the radical pair mechanism. There is also a modulation of transport rates and binding by the ICR mechanism. Liboff in the ICR model explains the acceleration of Ca^{+2} by cyclotron resonance which is generated by the acceleration of extremely low-magnetic field and there is increased flux Ca^{+2} ion (Liboff 1985). The formula by ICR model states the frequency and ion specificity and also explains the frequency-specific absorption of electromagnetic fields by the ions (Del Giudice et al. 2002). In addition to these mechanisms, the interaction between environmental impacts such as ionizing radiation (ultraviolet–UV) and the magnetic field influence as a repair mechanism has also been discussed by Galland- Pazur (Dicarlo et al. 1999).

UV-B and MF are the two aspects of radiation biology, and both have contradictory effects; UV-B irradiation has damaging effects while MF priming has beneficial effects on plant growth and development (Shine et al. 2011, 2012; Kataria et al. 2013, 2014a, 2017a, 2020a, 2021). The UV-B radiation and magnetic treatments caused alteration in the cell membrane, seed germination, plant photosynthetic efficiency, enzyme activities, and yield of the crop plants (Yinan et al. 2005; Shine et al. 2011, 2012; Kataria et al. 2014a, b, 2015, 2017a, 2020a, 2021).

7.3.1 Effect of Magneto-priming on Seed Germination, Growth, Photosynthesis, Nitrogen Fixation, Antioxidant Defense, and Yield under UV-B Stress

Once the seed has sown in the soil, faster germination and vigorous seedling growth are very important for seedling establishment and their ability to cope with continuously changing environment (Prajapati et al. 2020; Sarraf et al. 2020). The faster seed germination is very well documented as the primitive effect of magneto-priming. In a recent report, UV-B exposure for 1 h caused severe reduction in seed germination and early seedling growth parameters of soybean possibly due to reduced activities of total amylase, nitric oxide synthase (NOS), and nitrate reductase (NR). At the same time, they have also proved that magneto-priming of soybean seeds promotes the nitric oxide (NO) production via NOS and alleviates the UV-B stress in soybean seedlings (Raipuria et al. 2021). Further, perusal of literature also revealed that stimulation from magneto-priming exists in the plants till its maturity; thus, the magneto-priming (200 mT, SMF for 1 h) of soybean seeds increased the growth parameters such as plant height, leaf area, specific leaf weight, thickness of the midrib of trifoliate leaves, biomass accumulation, nitrogen fixation, photosynthetic performance, and crop yield in the presence of ambient and supplemental/enhanced UV-B stress (Fatima et al. 2021b; Kataria et al. 2017a, 2020a, 2021). Magneto-priming with SMF pretreatment and exclusion of solar UV-B components are the methods that put an end to the defense against the stress caused by ambient UV-B stress (Fatima et al. 2021b; Kataria et al. 2015, 2017a, 2020a, 2021). The comparison of soybean plants from magneto-primed groups with the respective unprimed ones even in the presence of ambient UV-B as well as enhanced or supplemental UV-B irradiations found that the rectifying effects of SMF were distinctive on overall growth of the plants (Fatima et al. 2021b; Kataria et al. 2015, 2017a, 2020a, 2021). The magneto-priming and solar UV-B exclusion have shown to accumulate higher biomass and increased leaf thickness in sorghum and amaranthus (Kataria and Guruprasad 2012b, 2014). The reduction in nitrogenase, nitrate reductase, nitrite reductase, and leghemoglobin (contents in the nodulated mung bean cultivars) confirmed that there is a negative impact of UV-B elevation on nitrogen fixation and assimilation (Choudhary and Agrawal 2014). Similarly, UV-B supplementation also reduced N_2 fixation in the two tropical leguminous crops *Phaselous mungo* and *Vigna radiate* (Singh 1997). However, the number and size of nodules, total protein, and Lb content was found to be reduced in soybean plants grown under ambient UV-B stress after exclusion of solar UV-B (Chouhan et al. 2008; Baroniya et al. 2014). Earlier studies on individual effects of SMF priming and solar UV exclusion in several crops indicated the stimulations in the activities of CA, NR, nitrogenase, and Rubisco along with the enhancement of plant growth, leaf area, biomass accumulation, and photosynthetic efficiency (Kataria et al. 2013, 2015, 2017a, 2020a; Kataria and Guruprasad 2012b, 2014, 2015). The SMF treatment has also shown the positive effect on the activity of nitrogen fixation under ambient UV-B stress as it enhances the leghemoglobin and heme-chrome content and also nitrogenase activity in the soybean root nodules (Kataria et al., 2017a, 2020a).

Ambient and supplemental UV-B were observed to increase the synthesis of UV-B-absorbing substances (UAS), reactive oxygen species (ROS) like superoxide radical (O_2•−) and hydrogen peroxide (H_2O_2), antioxidants like ascorbic acid and α-Tocopherol, and decrease the NR activity; subsequently, it results in a decreased rate of photosynthesis, biomass accumulation, and yield of the plants (Kataria et al. 2017a, 2020a, 2021). The SMF pretreatment caused reduction in the amount of ROS, MDA, proline, and UV-B-absorbing substances and the antioxidant enzymes such as SOD, GR, and POD activities similar to solar UV-B exclusion (Kataria et al. 2017a, 2020a, 2021). It indicates that the presence of UV-B stress caused the oxidative stress, and the exclusion of solar UV-B and SMF pretreatment to the seeds eradicates the requirement for the defense against harmful UV-B stress and leads to augmentation of primary metabolism and improves the crop yield (Kataria et al. 2017a, 2020a, 2021). Thus, crop yield is enhanced by SMF pretreatment and solar UV exclusion due to better leaf growth, leaf biomass, and higher efficiency of PSII, carbon and nitrogen fixation, higher DNA, RNA and protein content in the plants as compared to the plants receiving ambient UV-B and also supplemental or enhanced UV-B radiation (Kataria et al. 2017a, 2020a, 2021). Kataria et al. (2021) also found that SMF pretreatment increased the NO content and NR activity, higher efficiency of PSII, higher values of quantum yield of electron transport, relative amplitude of the I–P phase of Chl *a* fluorescence, performance indices, decreased intercellular CO_2 concentration, lower amount of UAS, ROS, and antioxidants that consequently improve the yield of soybean plants under ambient UV-B as well as supplemental UV-B stress. The recent reports on SMF pretreatment on yield of soybean plants in the presence of ambient or supplemental UV-B stress showed the enhancement in all the yield parameters namely number of pods, number of seeds/pods, pod and seed weight per plant and harvest index in the plants emerged from SMF-treated seeds as compared to the plants emerging from untreated seeds (Kataria et al. 2017a, 2020a, 2021).

7.4 Synchrotron Radiation and Its Use for Leaf Venation Imaging After Solar UV Exclusion and SMF Pretreatment

Synchrotron light sources are the scientific tools for basic and applied research in variety of fields ranging from material science, physics, chemistry, life science to archeological applications (Margaritondo 1988; Margaritondo and Meuli 2003).

During the past five decades, synchrotron source has evolved from first to fourth generation. The synchrotron light sources are composed of a storage ring which emits electromagnetic radiation (EMR) when the relativistic electron moves on a curved path with speed of light (Margaritondo 1988). The highly coherent radiation emitted from the synchrotron source can be used for phase sensitive imaging. Synchrotron radiation has been successfully used to observe the structural variations in leaf venation mainly the major conducting vein and adjoining minor veins of soybean plant under the influence of external environmental effects; the images of middle region of leaf midrib were obtained in intact third trifoliate leaves without any staining or sectioning (Fatima et al. 2016, 2017).

The morphological changes in leaf venation after exclusion of UV-B radiation and its impact on the leaf hydraulic activity of soybean plant have been studied using synchrotron-based X-ray imaging technique (Fatima et al. 2016). These authors reported that exclusion of solar UV-B caused 98% and 117% increase, respectively, in width of the mid-rib and minor veins of soybean third trifoliate leaves as compared to the leaves of plant grown under ambient UV-B stress. The novel phase contrast imaging technique with synchrotron source has also been applied to investigate the morphological changes in venation of leaves grown from soybean seeds pretreated with static magnetic field of different strengths from 50 to 300 mT (Fatima et al. 2017). The SMF strength of 200 mT for 1 h that caused considerable increase of 20% in thickness of the midrib was observed in soybean leaves (Fatima et al. 2017). These results encouraged the combined effect studies, involving soybean leaf midrib imaging grown from magneto-primed seeds in UV-exclusion conditions also; this study also showed the higher thickness of midrib and minor veins in soybean leaves as compared to the plants grown under ambient UV-B stress (Fatima et al. 2021b).

Leaf venation consists of the midrib or the major conducting vein and the associated minor veins which form a network for transporting water and nutrients to the plants from the roots. To understand the distribution of nutrient resources in plants, leaf venation is visualized and quantified using high-resolution X-ray Phase-Contrast Imaging (PCI) (Fatima et al. 2016). Compared to the conventional methods, X-ray PCI is a fast and novel method to image the leaf venation in intact leaves as plant leaves are thin weakly absorbing samples (Fatima et al. 2016). The leaf venation network is linked to the rate of photosynthesis in plants through the leaf hydraulic mechanism. Water transportation is the vital leaf growth parameter and shows an increment with the SMF pretreatment of the seeds which are also indicated by the midrib enhancement. X-ray PCI has been used to image the midrib and the associated higher order minor veins to indicate the enhancement in these veins in soybean with the SMF treatment, UV exclusion from the solar radiation and in the combination of these two phenomena (Fatima et al. 2016, 2017, 2021b). In order to visualize and quantify the leaf venation from the PCI images obtained at the synchrotron, single-distance phase retrieval has also been applied for soybean leaves which are comprised of light-absorbing element. These structural changes in leaves obtained from X-ray PCI are associated with the photosynthetic rate and stomatal conductance which thus showed and improved plant productivity after the SMF treatment and UV exclusion (Fatima et al. 2016, 2017). Detailed investigation has been performed to correlate leaf venation and leaf hydraulic mechanisms by imaging major and minor vein up to 3°. These studies conducted with synchrotron-based X-ray PCI showed that the two parts of radiation biology namely magnetic field treatment with low flux densities and solar UV exclusion have positive effects on leaf venation and plant growth parameters such as leaf biomass and thickness of midrib and minor veins of third trifoliate leaves of soybean along with higher rate of photosynthesis under both individually and in the combination (Fatima et al. 2016, 2017, 2021b).

7.5 Conclusion and Future Perspectives

Current projected elevated levels of UV-B rays and its impact on agricultural crops have become a major concern to the plant biologists. The enhanced UV-B rays hamper the crop productivity by altering the developmental rates, leaf photosynthesis (photosystems, thylakoid, and grana membrane integrity), defense compounds like flavonoids, phenolic compounds, or waxes. In other direction, current UV-B levels are strong enough to induce ROS generation which triggers the antioxidant defense systems which also results in retarded growth and development of crop plants. In order to cope with UV-B stress, growing the plants under solar UV exclusion and SMF pretreatment of seeds, both improve the performance under ambient UV-B or enhanced UV-B stress. Both strategies improve the plant growth, biomass accumulation, nitrogen fixation through higher leghemoglobin, hemechrome content, nitrogenase activity in the root nodules, higher efficiency of PSII, and rate of photosynthesis which eventually results in higher crop yield. Thus, SMF pre-sowing treatment and solar UV-B exclusion alter the plant metabolism and provide protection to the plants from UV-B stress. As per the available reports, increased crop yield by SMF and solar UV exclusion is due to the better leaf growth, leaf biomass, efficiency of PS II, higher carbon and nitrogen fixation, higher the nucleic acid and protein content in the plants in comparison to untreated ones grown under UV-B stress conditions. Hence, magneto-priming of seeds before sowing and exclusion of solar UV-B can be used as potential strategies for the protection of plants to provide the tolerance against ambient UV-B stress. However, molecular mechanisms involved in magneto-priming-based or UV-B exclusion-based improved performance of the plants, are not fully understood. Detailed studies in this direction need to be conducted which can shed the light upon hidden molecular mechanism proving UV-B stress tolerance in both cases. Also, genes regulating the leaf growth, photosynthesis, nitrogen fixation in model plants and crops can be explored and characterized to be involved in the UV-B stress tolerance.

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