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Growth and development responses to UV-B exclusion in crops

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Abstract

UV-B radiation affects crop plants. Growing interest has been shown in studying the effects of UV-B radiation exclusion on crops since 1993. This article summarized the general consequences of UV-B radiation exclusion on crop plants from the aspects of plant morphology, growth and development. UV-B exclusion has promoting effects on plant height, internode and leaf size. UV-B exclusion increases root biomass and stimulates nodulation of legume crops with increased number and size of nodules and enhances the leghemoglobin. Higher levels of α-tocopherol is found in UV-B plants, which plays an important role in translocating photoassimilates from the leaves to the roots. UV-B exclusion could be a useful tool for physiologists and molecular biologists to further address mechanisms involved in UV-B radiation damage in crop plants.

Keywords: UV-B exclusion; Plant morphology; Growth; Development.

Introduction

Since the discovery of the Antarctic 'ozone hole' and general depletion of the stratospheric ozone layer in the mid-1980s, a substantial number of studies have been intensively conducted over the past several decades to assess the potential impacts of enhanced ultraviolet-B radiation on crop plants under greenhouse, growth chamber cladding materials conditions or field conditions (Biggs et al., 1981; Teramura et al., 1990; Allen et al., 1998; Rathore et al., 2003; Yannarelli et al., 2006; Peng et al., 2010; Kataria et al., 2012a; Liu et al., 2013; Alonso et al., 2015).

While the laboratory and glasshouse studies or field studies with supplemental/ enhanced UV-B provide information on mechanisms and processes of UV-B action, interest has been shown in studying the effects of UV-B radiation exclusion on crops since 1993 (Lingakumar et al., 1999; Krizek et al., 2005; Zhang et al., 2014), because the UV-B exclusion studies seem to be more appropriate to identify the most sensitive or insensitive variety to the ambient level of solar UV radiation and for the selection of best suited variety for a given latitude and have greater significance under a tropical environment where the plants receive higher amount of UV radiations (Lingakumar et al., 1993). Thus, this method will provide more realistic assessments of sensitivity of plant species or varieties to current level of UV radiation and more valuable information about the natural adaptation of crop plants (Kataria and Guruprasad, 2012b). This minireview summarized available information to researchers regarding the general consequences of UV-B radiation exclusion on crop plants from the aspects of plant morphology, growth and development with an aim for agronomists, physiologists and molecular biologists to reappraise the effects of UV-B radiation on crop plants in light of improved mechanistic understanding of UV-B effects.

Responses of plant growth to UV-B exclusion

Outstanding work of exclusion of UV-B radiation on plant morphology and growth have been conducted by Indian scientists led by Dr. Kataria and Dr. Guruprasad from Nuclear Research Laboratory, Indian Institute of Agricultural Research, India (Kataria and Guruprasad, 2012 b). Lingakumar et al. (1993) found that Cowpea *Vigna unguiculata* (L.) Walp. seedlings were 40% taller at 15 days after sowing (DAS) in the absence of UV-B, while Kataria and Guruprasad (2012b) showed an 18% increase in stem length when grown for 3 days in a growth chamber free of UV-B. They attributed the UV-B-induced reduction in cowpea stem length to the presumed destruction of endogenous growth hormones.

In a field UV-B exclusion experiment using polyester films covering hut-shaped structures, Pal et al. (1997) observed that mung bean *Vigna radiata* (cv. PS-16) height and stem weight was 37% and 55% greater, respectively, at 65 DAS under the UV-B screen. However, at 80 DAS, they found that maize *Zea mays* L. (cv. SM-600) was affected little. Height of maize was only 5% greater and stem weight was 7% less under UV-B exclusion.

For four cucumber (*Cucumis sativus* L.) cultivars, Krizek et al. (1997) showed that, at 19–21 DAS, the average main shoot length was 27% greater for exclusion of UV-B only. Similarly, the effects of these exclusions on guar bean (*Cyamopsis tetragonoloba*), mung bean and black gram (*Vigna mungo*) were measured by Amudha et al. (Krizek et al., 2005). They found that, at 50 DAS, guar bean was 21% taller and mung bean was 15% taller, for the exclusion of UV-B radiation. However, there was no difference in the height of the black gram among treatments. Guruprasad et al. (2007) found that height increase of soybean (cv. JS7105), was 30% for UV-B exclusion of solar radiation. At 70 days after emergence, Dehariya et al. (2012) found plant height of cotton (*Gossypium hirsutum* L.) var.Vikram was increased 60% for UV-B exclusion. In a study of four cultivars of wheat (*Triticum aestivum* L.), Kataria and Guruprasad (2012b) reported maximum height increases at maturity of 20% for UV-B exclusion.

In soybean, Biggs et al. (1981) found an 80% average increase in height of 19 cultivars of 4-week-old soybean when exposed to no UV-B radiation compared to 2.34 mW m^{-2} UV-B as weighted by a DNA action spectrum. Total height of soybean (cv. Williams) was 2.5 times greater for young plants grown under low pressure sodium lamps (deficient in blue, UV-A and UV-B wavelengths) than for plants grown at the same photosynthetic photon flux density, PPFD (500 μ mol photon m^2s^{-1}) under broad-spectrum daylight fluorescent lights with a small amount of UV-B radiation between 310 and 320 nm (Britz and Sager, 1990). Similar increases in soybean (cv.McCall) mainstem length and average internode lengths were reported by Wheeler et al. (1991). All these studies mentioned above indicate that the UV-B exclusion effect is likely dependent on plant species.

Baroniya et al. (2013) showed that intraspecific variation in crop growth and yield of eight soybean varieties to ambient UV-B radiation by exclusion of UV-B alone under field conditions. The exclusion of solar UV-B enhanced the vegetative growth (plant height and leaf area), total biomass accumulation and yield (number of seeds and seed weight) of all the varieties as compared with those grown under ambient UV-B and suggested that the ambient level of UV-B radiation caused some active oxygen species to accumulate, which in turn retarded the growth, development and yield of soybean varieties. Zhang et al. (2014) found a similar response to soybean and proposed that part of the height increases likely resulted from the photomorphological effects of UV-B exposure rather than all the increase due to lack of damage associated with no exposure to UV-B radiation. They also found exclusion of UV-B radiation caused elongated internodes on the plants, which resulted in greater plant height and a slight increase in the number of nodes with increasing extent of UV radiation exclusion.

Pinto et al. (2002) showed that bean (*Phaseolus vulgaris*) plants grown under ambient UV radiation had almost 60% more nodules per plant than plant deprived of UV-B. Rinnan et al. (2005) also found a 30% increase in the root biomass in *Vaccinium uliginosum* under reduction of UV-B radiation in an arctic heath in northern eastern Greenland. Chouhan et al. (2008) indicated that UV-B exclusion increased the number and size of nodules of soybean plants and Baroniya et al. (2014) indicated that exclusion of UV-B significantly enhanced the growth of the aerial parts as well as the growth of the below ground parts in all of the six soybean varieties.

Therefore, UV-B exlusion has promoting effects on plant height, internode and leaf size. Enhanced UV-B reduced leaf area and leaf thickness (indicated by specific leaf weight) has been reported in maize, *Amaranthus tricolor* and sorghum varieties (Correia et al., 1999; Kataria and Guruprasad, 2012a), while specific leaf area and length of internodes and petiole in Indian cress (*Tropaeolum majus*) were unaffected by enhanced UV-B radiation (Germ et al., 2015). The decrease in leaf thickness may have increased the UV-B penetration within leaves and decreased photosynthetic rates and dry weight accumulation. Increased epidermal cell wall thickness was also found in loblolly pine (*Pinus taeda*) and Scots pine (Laakso et al., 2000). Qi et al. (2003) found that there was a good correlation between total leaf thickness and total concentration of leaf UV-B absorbing compounds in southern broadleaf tree species in USA and a strong presence of UV-absorbing compounds in the upper and lower epidermis, the vascular bundles and the leaf hairs, if present. However, the main site of UV-B attenuation took place within the upper leaf epidermis (Qi et al., 2003). However, how the absence of UV-B regulates growth and what mechanism invovled at physiological and molecular level is poorly understood.

Responses of plant development to UV-B exclusion

Pinto et al. (2002) found that exposure of bean (*Phaseolus vulgaris*) plants grown in green house, where UV-B is low to the ambient level of UV-B light stimulated nodulation more than 2.5 fold. Chouhan et al. (2008) showed that exclusion of UV radiations significantly enhanced the leghemoglobin (a protein that plays an important part in the fixation of nitrogen in the nodules) content in the nodules on fresh weight basis with 25% higher amounts of leghemoglobin present in the nodules after the exclusion of UV-B radiation. Analysis by native and SDS-PAGE showed high intense bands of leghemoglobin after the exclusion of UV-B as compared to control in the root nodules. It is evident that absence of UV-B alters the metabolism in soybean in favor of primary metabolism especially in enhanced synthesis of proteins.

Guruprasad et al. (2007) found that increases in plant height, leaf size, leaf dry weights and changes in branching pattern in soybean grown under low UV-B, but little effects on chlorophyll or photosystem II. They suggested that photomorphogenic mechanisms rather than photosynthesis were impacted by absence of UV-B. They also suggested that the equilibrium between the red light (Pr) and far-red light (Pfr) forms of phytochrome might be changed since phytochrome has absorption in the UV region. In fact Pr and Pfr absorb UV-A similarly, but UV-B is absorbed slightly better by the Pr form (Lagarias et al., 1987). It is unlikely that this would shift the photoequilibrium sufficiently to alter phytochrome activity and subsequent phytohormone synthesis. Zhang et al. (2014) indicated that while leaf photosynthetic rates were lower for plants with minus UV-B treatment, the lower photosynthetic rate did not result in total biomass and reproductive yield (pod). This may be due to the morphological changes induced by UV-B exclusion which resulted in a larger leaf area and elongated leaf petioles than would enable more light interception per plant.

Recent field experiment conducted under tropical climate for assessing the effect of ambient UV-B by exclusion of UV components on the growth, photosynthetic performance and yield of C_3 (cotton, wheat) and C_4 (amaranthus, sorghum) plants indicated that all the four plant species responded to UV exclusion by a significant increase in plant height, leaf area, leaf biomass, total biomass accumulation and yield and exclusion of UV-B in particular significantly enhanced the net photosynthetic rate, stomatal conductance and activity of Rubisco. They also found that additional fixation of carbon due to exclusion of ambient UV-B was channeled towards yield as there was a decrease in the level of UV-B absorbing substances and an increase in soluble proteins in all the four plant species (Kataria et al., 2013; Kataria and Guruprasad, 2014). This indicates that there might be a same mechanism involved to UV-B exlusion for both C_3 and C_4 plants.

Baroniya et al. (2014) indicated that nitrate reductase activity (NRA) was significantly reduced, whereas leghemoglobin (Lb) content, total soluble protein, net photosynthesis (Pn) and α-tocopherol content were enhanced after UV exculsion. They also found that the exculsion of UV-B enhanced all parameters to a larger extent than the exclusion of solar UV-B in four of the six varieties and a significant inverse correlation between the NRA and the number of nodules per plant was observed.

The number of nodules per plant in the bean grown in conditions of ambient UV radiation was higher than that on plants deprived of UV-B (Pinto et al., 2002). Chouhan et al. (2008) found that ambient UV-B reduced the number and size of nodules, total protein and Lb content in the soybean. However, Shiozaki et al. (1999) found that UV (300-400 nm) applied to leaves increased the amounts of nodulation and symbiotic N_2 fixation in pea plants. Baroniya et al. (2013) reported that UV-excluded soybean plants had higher levels of α-tocopherol, which plays an important role in translocating photoassimilates from the leaves to the roots (Hofius et al., 2004).

Zhang et al. (2014) found that at the R_2 stage there was no significant difference between the soybean fresh weight concentrations of indole acetic acid (IAA) in unfolding, expanding leaves of plants among the three levels of UV. However, at the R_6 stage the IAA concentration was 4-fold higher in the no UV exclusion plants than in the minus UV-B treatments. The sampled stages for hormone analysis may have been too late, especially at the R_6 stage and because auxin may play more of a role in internode tissues than unfolding leaves. Furthermore, IAA usually affects plant height by increasing cell numbers (through cell division). They then suggested that the elongation process was not through cell division, but rather through cell elongation, which is affected more by gibberellin (GA) (Umezaki et al., 1991; Luo et al., 2006; Zhu et al., 2006). Ambient UV-B affected the biomass partitioned to tubers and increased root diameter and root fresh weight of radish (Zavalla and Botto, 2002).

The above results mentioned indicated UV-B exclusion stimulates nodulation of legume crops with increased number and size of nodules and enhances the leghemoglobin. Higher levels of α-tocopherol induced by UV-excluded plays an important role in translocating photoassimilates from the leaves to the roots. Findings also proposes that dicots are more sensitive than monocots while no great difference in sensitivity between C_3 and C_4 plants. Thus, exclusion of solar UV-B will have agricultural benefits in both C_3 and C_4 plants under tropical climate.

Conclusions and future research

UV-B exlusion has promoting effects on plant height, internode and leaf size. UV-B exclusion increases root biomass and stimulates nodulation of legume crops with increased number and size of nodules and enhances the leghemoglobin. Higher levels of α-tocopherol is found in UV-B plants, which plays an important role in translocating photoassimilates from the leaves to the roots. Since plants possess an array of adaptive responses to UV-B that allow them to prevent, mitigate or repair UV-B damage and UV-B radiation can be a regulator of plant growth, morphology and development as well as a potent inducer of protective mechanisms (Suchar and Robberecht, 2014; Robson et al., 2015), it is essential for future studies to make an extensive investigation of the status of physiological, biochemical and molecular consequences after exposure to natural levels of UV-B and exclusion of UV-B.

However, most studies in the past several decades were conducted indoor using a growth chamber or greenhouse and field conditions in which plants were exposed to enhanced or high UV-B radiation and relatively lower levels of photosynthetically active radiation (PAR: 400-700 nm). Responses of plants in controlled conditions may differ from those in the field conditions, because of alterations in the natural spectral balance of UV-B and PAR (Caldwell et al., 2007) and the balance of damage and repair mechanisms (Krizek et al., 2005). While the laboratory and greenhouse studies provide information on mechanisms and processes of UV-B action, only field studies can provide realistic assessments of what will happen as the stratospheric ozone layer thins (Pal et al., 1997).

Because of its more realistic assessments of sensitivity of plant species or varieties to current level of UV radiation and more valuable information about the natural adaptation of crop plants by UV-B exclusion, there is a need to reappraise the effects of UV-B radiation on plant morphology, growth abd development in light of improved mechanistic understanding of UV-B effects. In using this new approach, we suggest to investigate the following research under UV-B exclusion conditions.

(1) Differentiating the main UV-absorbing compounds and non-enzymatic antioxidants;

(2) Assessing the changes of oxidative status and the response of the main antioxidant enzymes;

(3) Examining the responses of the main endogenous phytohormones activities;

(4) Identifying genetic consequences caused by full-season UV-B radiation;

(5) Evaluating the effects of UV-B radiation on quality and quantity of produce and the environmental load resulting from production.

These researches, in our opinions, will fill in the knowledge gap regarding the photocontrol mechanisms of UV-B to crop plants under field conditions and provide insights into the ecological role of UV perception by plants and breeding and management strategies for agricultural production.

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