

Influence of PAR and UV-A in Determining Plant Sensitivity and Photomorphogenic Responses to UV-B Radiation

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ABSTRACT

The role of photosynthetically active radiation (400-700 nm) (PAR) in modifying plant sensitivity and photomorphogenic responses to ultraviolet-B (280-320 nm) (UV-B) radiation has been examined by a number of investigators, but few studies have been conducted on ultraviolet-A (320-400 nm) (UV-A), UV-B and PAR interactions. High ratios of PAR-UV-B and UV-A-UV-B have been found to be important in ameliorating UV-B damage in both terrestrial and aquatic plants. Growth chamber and greenhouse studies conducted at low PAR, low UV-A and high UV-B often show exaggerated UV-B damage. Spectral balance of PAR, UV-A and UV-B has also been shown to be important in determining plant sensitivity in field studies. In general, one observes a reduction in total biomass and plant height with decreasing PAR and increasing UV-B. The protective effects of high PAR against elevated UV-B may also be indirect, by increasing leaf thickness and the concentration of flavonoids and other phenolic compounds known to be important in UV screening. The quality of PAR is also important, with blue light, together with UV-A radiation, playing a key role in photorepair of DNA lesions. Further studies are needed to determine the interactions of UV-A, UV-B and PAR.

Abbreviations: BSWF, biological spectral weighting function; CA, cellulose acetate; CHS, chalcone synthase; CPD, cyclobutane pyrimidine dimer; CRY, cryptochrome; HPS/DX, high-pressure sodium/deluxe; MH, metal halide; PAR, photosynthetically active radiation (400-700 nm); PSII, Photosystem II; RAF, radiation amplification factor; UV-A, ultraviolet-A (320-400 nm); UV-B, ultraviolet-B (280-320 nm); 6-4 PP, pyrimidine (6-4) pyrimidone dimers; 8-oxodGuo, 8-oxo-7,8-dihydro-2'-deoxyguanosine.

INTRODUCTION

Since the early 1970s there have been intensive efforts to assess the biological impact of stratospheric ozone depletion caused by chlorofluorocarbons and other anthropogenic sources. Comprehensive reviews have been written on the effects of ambient and supplemental ultraviolet-B (280-320 nm) (UV-

B) radiation on terrestrial plants (1-16). Several excellent reviews have also been written on the impact of solar UV radiation on aquatic organisms (12, 16-18).

Increases in biologically effective UV radiation due to decreases in total ozone have been observed in Antarctica during the formation of the ozone hole as well as in the Northern Hemisphere (19). Recent changes in surface UV solar radiation and stratospheric ozone have also been reported at a high Arctic site, although it is still too early to make trend estimates. Current levels of stratospheric ozone are at the lowest point since measurements were first taken in the 1970s; global terrestrial UV-B radiation levels range between 0 and 12 kJ m⁻² day⁻¹, with regions near the Equator and midlatitudes receiving higher doses (15).

Research on UV-B effects on crop plants has been conducted largely with species from temperate latitudes (see reviews in Krupa et al. [4], Day [9], Caldwell et al. [13], Flint et al. [14], Kakani et al. [15] and Corlett et al. [20]). If sensitive cultivars are avoided, crop yield of these species may not be greatly reduced (7). Much less is known, however, about crops and ecosystems in tropical regions in areas of intense solar UV-B radiation (21,22).

The fact that there are many indirect effects of UV-B radiation as well as numerous interactions with other environmental factors (4,10,12-15,23-26) makes UV-B research highly complex. Results from short-term studies on UV effects cannot necessarily be extrapolated to long-term assessments. In contrast to studies in other fields of environmental research, such as air pollution (4), the database of realistic and ecologically relevant UV-B studies is extremely limited, and the interpretation of published data on UV-B experiments is often equivocal (7,13,15).

The role of photosynthetically active radiation (400-700 nm) (PAR) in modifying plant sensitivity and photomorphogenic responses to UV-B radiation has been examined by a number of investigators (27-31), but few studies have been conducted on ultraviolet-A (320-400 nm) (UV-A), UV-B and PAR interactions (32-34). To ameliorate the effects of elevated UV-B radiation, it is important to have a good understanding of how these various wavelengths act in concert with one another to influence plant growth and development.

The objective of this article is to review recent literature on the interactive effects of UV-A, UV-B and PAR in influencing plant sensitivity to UV-B radiation and photosynthetic responses; discuss the role of UV-A and blue wavelengths in repairing DNA damage in terrestrial and aquatic plants; review current knowledge of UV photoreceptors in photomorphogenesis; and describe natural UV-B defense mechanisms.

COMPARISON OF GREENHOUSE, GROWTH CHAMBER AND FIELD STUDIES

Numerous UV-B enhancement studies on terrestrial plants have been conducted under laboratory, growth chamber, greenhouse and field conditions (see reviews in Ballare et al. [8], Day [9], Searles [10],

Bjorn [11], Day and Neale [12], Caldwell et al. [13], Flint et al. [14], Kakani et al. [15] and Vincent and Roy [16]). Results from greenhouse or growth chamber studies and field studies on UV-B effects are often conflicting (14,21) or difficult to interpret, because of unrealistically high UV irradiation levels, inadequate levels of UV-A, low PAR or other technical difficulties (14,15,34-40). In general, one observes a reduction in total biomass and plant height with decreasing PAR and increasing UV-B.

Outdoor supplementation systems have increased in popularity during the past few years because they provide a method of study that creates only small alterations in the microclimate (2,15,39,40). However, they differ greatly in their methods of operation, equipment, UV-B exposure regime and experimental design (2,14,15,35, 37-39,41-43).

UV-B studies conducted on natural ecosystems in Hawaii indicate that species from high elevations, exposed to high levels of ambient UV-B, were generally more resistant to enhanced UV-B than corresponding plants grown at low elevations, when both groups of plants were grown in the greenhouse under supplemental UV-B (44).

PLANT RESPONSE TO AMBIENT SOLAR UV RADIATION

To avoid many of the problems inherent in UV enhancement experiments, there has been growing interest in the use of systems that exclude or attenuate the UV-B component of natural solar radiation (8,10,25,45-58). To date, relatively few species or cultivars have been investigated under UV-exclusion conditions. Thus, our knowledge of the effects of ambient solar UV-B and UV-A radiation is meager. The results of UV-exclusion studies indicate that plants vary widely in their response to ambient UV-B (52,57). In some species (e.g. cucumber, mung bean, New Zealand spinach and "New Fire" lettuce) growth is inhibited by solar UV-B (48-51). In some species (e.g. tomato and others) growth is promoted (49,59), whereas in others (e.g. cotton, oats) it is unaffected (48,49).

Qualitative effects of solar UV-A radiation on higher plants have been reported (see Tezuka et al. [60] and references therein), but quantitative data are minimal. Recent UV-exclusion studies conducted at Beltsville, MD, on cucumber (49) and a red-pigmented lettuce (51) indicate that ambient UV-A greatly inhibits leaf enlargement, stem elongation and biomass production over and above that under ambient UV-B.

In conducting UV-exclusion studies, it is important to obtain measurements of UV-A, UV-B and PAR transmission through the filter materials. Measurements of total radiation or infrared radiation with a pyranometer above and below the filters should also be made because slight differences in transmission through different exclusion filters can cause serious confounding effects (14). Although cellulose acetate (CA) has been widely used in UV-B-exclusion studies, recent evidence indicates that CA toxicity (manifested as stunting and chlorosis in cucumber [*Cucumis sativus* L.]) may occur possibly as a result of outgassing of dibutyl phthalate, known to be used as a plasticizer in the manufacture of CA or some

breakdown product (58). To avoid possible confounding effects from the use of CA (58,61) and to obtain maximum transmission of UV and PAR (8,9,12-14,61), it is preferable to use Aclar (polychlorotrifluoroethylene) or Teflon FEP (a copolymer of tetrafluoroethylene and hexafluoropropylene) in UV-exclusion studies. Other materials have also been used to alter the spectral cutoff (58).

One method of UV-B attenuation that has been used successfully is to construct an O₂-containing envelope of UV-transparent Plexiglas to reduce the amount of UV-B. These "O₂ cuvettes" have been placed over growth chambers outdoors in Portugal to simulate ambient and elevated UV-B conditions in Germany (47). This system is rather expensive, however, for most investigators and must be monitored for possible O₂ leaks.

GENOTYPE DIFFERENCES IN UV-B SENSITIVITY

Species and cultivars within these species may differ widely in their response to UV-B (62-64). Monocots appear to be generally more resistant to UV-B enhancement than dicots (50). Native species appear to be more resistant to elevated UV-B radiation than crop plants in terms of changes in biomass reduction, but both groups may show subtle changes in shoot elongation and leaf size. These morphological changes may have important consequences for natural ecosystems by altering the competitive balance in mixed communities, with more UV-B-resistant species replacing UV-sensitive ones.

ROLE OF UV PHOTORECEPTORS IN PHOTOMORPHOGENESIS

The importance of UV radiation in photomorphogenesis has become increasingly recognized (65). In recent years it has become clear that plants have several UV photoreceptors and that UV exerts its action through the coaction of UV photoreceptors and photoreceptors in the visible region (65-70). It is generally believed that there are three main sensor pigments in higher plants: phytochrome (operating predominately in the red-far-red spectral range), cryptochrome (CRY1, operating in the blue-UV-A spectral range) and a UV-B photoreceptor with maximum action at 280 nm (and no action at wavelengths longer than 350 nm) (66).

Plants are thought to have at least two types of blue light receptors, CRY and phototropin (70). CRY are 70-80 kD flavoproteins that are similar in structure to DNA photolyase but lack photolyase activity (70). CRY act concurrently with phytochromes to mediate photomorphogenic responses such as inhibition of stem elongation, stimulation of leaf expansion, photoperiodic control of flowering, entrainment of the circadian clock and regulation of gene expression (70). They have been found throughout the plant

kingdom. Phototropins mediate photomovement responses such as phototropism, chloroplast relocation and stomatal opening.

Numerous studies have been conducted to elucidate the mode of action among these three sensor pigments (66), and several model systems have been proposed (69). It is generally believed that these different photoreceptors, acting in some cases at different stages in plant development, work together to provide protection against damaging UV-B wavelengths (69).

Photophysiological, biochemical and genetic data indicate that plants contain a number of different blue-UV-B photoreceptors. However, molecular information on a blue-UV-A photoreceptor in plants is meager (70,71). The possibility that the chromophore could be a carotenoid has been considered (72) but has meager experimental support. Studies involving the use of Norflurazon (SAN 9789) and Difunon (EMD-IT-5914) to inhibit carotenoid biosynthesis also argue against this possibility.

Several workers have suggested that the UV-B photoreceptor is probably a protein with flavin or pterin chromophores (or both) (69,70,72,73). Pterins are thought to be a particularly strong candidate (69,70). Recent experiments indicate that there is a synergistic interaction among UV-B, UV-A and blue light signal transduction pathways (68-70), but there is only meager information published specifically on UV-B signal transduction (70).

Lin et al. (74) demonstrated that overexpression of CRY1 resulted in hypersensitivity to blue, UV-A and green light for the inhibition of hypocotyl elongation in *Arabidopsis*; transgenic plants overexpressing CRY1 showed increased anthocyanin accumulation in response to blue, UV-A and green light in a fluence-dependent manner. They concluded that CRY1 is a photoreceptor mediating blue light-dependent regulation of gene expression. Lin et al. (75) also found that expression of an *Arabidopsis* CRY gene in tobacco results in hypersensitivity to blue, UV-A and green light. Ninu et al. (76) reported that CRY1 controls tomato development in response to blue light.

INTERACTIVE EFFECTS OF UV-A, UV-B AND VISIBLE RADIATION

There are numerous reports on the separate effects of UV-A, UV-B and visible radiation on terrestrial plants, but relatively little has been published on the combined interactions of these wavelengths. One of the difficulties in drawing extrapolations from early UV-B studies in plant growth chambers to what might occur under field conditions is that the PAR levels obtained in these controlled-environment experiments using artificial sources (e.g. fluorescent and incandescent lamps) were generally quite low (14). Use of high-intensity discharge lamps (30,77,78) and other sources of high PAR should enable more meaningful UV-B growth chamber studies to be conducted.

The balance of irradiation in different wavebands (UV-B, UV-A and visible) has been shown to have a large bearing on plant sensitivity to changes in UV-B (21,27,29,32-34,78-82). Adamse and Britz (83) reported that ambient PAR (ca 1000-1600 $\mu\text{mol m}^{-2} \text{s}^{-1}$) was able to ameliorate the effects

of UV-B radiation levels as high as $18 \text{ kJ m}^{-2} \text{ day}^{-1}$. Dai et al. (21) reported that daily exposure of rice plants to enhanced UV-B radiation ($13 \text{ kJ m}^{-2} \text{ day}^{-1}$) had a significant inhibitory effect on growth and dry matter production in the greenhouse but no significant effect on field-grown plants given the same level of UV-B enhancement for four successive seasons at the International Rice Research Institute in the Philippines. They attributed this discrepancy to the higher amount of UV-A radiation in the field and the proportionally greater amount of irradiance in the 290-303 nm region in the greenhouse. Their measurements indicated that the ratio of UV-A to biologically effective UV-B radiation in the field was 7.5 times greater than in the greenhouse (21).

Caldwell et al. (32) reported that soybean plants exposed to elevated UV-B in the field under a modulated system only showed a reduction in biomass when the PAR and UV-A were reduced to below half of the full-sunlight levels. When PAR was low, UV-A was found to be particularly effective in mitigating UV-B damage. However, when PAR was high, substantial UV-A did not appear to be required for mitigation of UV-B damage.

Although the impact of PAR levels on UV-B sensitivity is well documented, relatively few studies have examined the influence of the source of PAR on plant response to UV-B irradiation (30,77, 78). In growth chamber experiments on cucumber (*C. sativus* L.) grown under $600 \mu\text{mol m}^{-2} \text{ s}^{-1}$ of PAR provided by metal halide (MH) or high-pressure sodium/deluxe (HPS/DX) lamps, Krizek et al. (77) observed greater UV-B induced chlorosis in leaves of the UV-B-sensitive cultivar 'Poinsett' under HPS/DX lamps than under MH lamps. They attributed these differences to the lower amounts of UV-A and blue radiation available for photorepair of UV-B damage under HPS/DX lamps. Exposure of plants to $18.2 \text{ kJ m}^{-2} \text{ day}^{-1}$ of biologically effective UV (weighted with a weighting function) ($\text{UV}^{\text{sub BE}}$) decreased height, dry weight and leaf area in both UV-B-sensitive Poinsett and UV-B-insensitive 'Ashley' cucumber. Apart from chlorosis, there were no interactive effects of UV-B, PAR source or cultivar on any of the growth parameters measured, suggesting that the growth response of cucumber seedlings to UV-B is unaffected by PAR source or cultivar.

Studies on UV-B enhancement in the field have had mixed results. In some cases there have been reports of reduced productivity; in other cases UV-B treatment has been found to have no effect on yield (84,85). Allen et al. (86) have pointed out that in most of these field studies a "square-wave" UV-B irradiation system was used, with lamps producing a constant level of UV-B enhancement based on a chosen O_3 depletion scenario for a particular day of the year and assuming cloud-free conditions. Fiscus et al. (84) have suggested that in many of these field studies the supplemental UV-B irradiance represented a much larger O_3 depletion scenario than stated: first, because of an overestimation of the model used to calculate the desired UV-B enhancement levels and second, because there was no adjustment of supplementary UV-B levels with change in season and weather conditions.

Without making adjustments in the supplemental UV-B levels, the ratio of UV-B to PAR and UV-A is higher and more variable on average than that observed naturally or after O_3 depletion (86). Caldwell and Flint (41) have pointed out that the use of a modulated UV-B irradiation system avoids these problems by continually monitoring ambient UV-B and adjusting supplemental irradiance accordingly, ensuring that realistic ratios of UV-B to PAR and UV-A are maintained during the day and

during the season. Variations in the ratios of UV-B-UV-A and UV-B-PAR may also have a significant biological impact on aquatic organisms (16,87). Vincent and Roy (16) have suggested that changes in the UV-B-UV-A balance could affect some species more severely than others.

IMPORTANCE OF UV-A AND BLUE WAVELENGTHS IN REPAIRING UV-B-INDUCED DNA DAMAGE

Direct absorption of UV-B photons by the DNA bases has been shown to induce two major DNA damage products in plants: cyclobutane pyrimidine dimers (CPD) and, at a lower frequency, pyrimidine(6-4)pyrimidone dimers (6-4 PP) (88-92). Plants have two primary mechanisms of coping with DNA damage, viz., photoenzymatic repair (i.e. light repair) requiring photolyase and nucleotide excision repair or dark repair requiring adenosine triphosphate (90-93). Light repair is rapid and generally occurs within a few hours; dark repair is much slower.

Plants must cope with UV-B radiation by balancing damage, repair and acclimation (94). Solar-induced CPD accumulation has been detected in terrestrial plants and aquatic plants (phytoplankton and macrophytes) from a wide range of latitudes, indicating that CPD induction can exceed repair rates (95). High levels of UV-A radiation can ameliorate UV-B damage to DNA through photoreactivation (90,96,97). In addition to UV-A, blue wavelengths have also been shown to be important in photorepair (89,93,98). Hada et al. (99) determined the action spectra for photorepair of CPDs and observed maximum effectiveness at 400 nm.

Photolyases are DNA repair enzymes that use energy from UV-A or blue light (400-500 nm) to energize the direct reversal of pyrimidine dimer bonds (89). Enzyme-catalyzed reversal of CPDs in situ has been found in a wide range of terrestrial and aquatic plants as well as in many animals (89,97). CPD repair in macrophytes under artificial light has been shown to be similar to that in reduced sunlight (95). Light-dependent reversal of CPDs in macrophytes is saturated at relatively low photon levels; similar results have been obtained in terrestrial plants (100). Takayanagi et al. (101) reported that alfalfa seedlings grown outdoors were more resistant to UV-induced DNA damage than plants grown in a UV-free environmental chamber. The level of PAR has been shown to be important in UV repair (102). Ries et al. (102) reported that UV-damage-mediated induction of homologous recombinations in *Arahidopsis* depended on the PAR level.

There are several excellent reviews on the molecular biology of plants exposed to UV-B radiation and the interaction with other stresses (93,103). Ballare (104) has pointed out the need for understanding the molecular basis of UV adaptation and has reviewed recent advances that have been made at the molecular level. Several workers have reported on changes in gene expression in response to UV-B-induced stress (105-107).

Various approaches have been developed for quantifying oxidative DNA damage in the environment. The typical approach for quantifying CPD and 6-4 PP has been to use an enzyme-linked immunosorbent assay with monoclonal antibodies (108). Mitchell et al. (108) have developed a novel radioimmunoassay for quantifying 8-oxo-7,8-dihydro-2'-deoxyguanosine (8-oxodGuo) in DNA in dosimeters deployed at various depths in the ocean or at the surface in the Antarctic. The frequency of both CPD and 8-oxodGuo decreased with depth, but CPD induction was attenuated at a faster rate than that of 8-oxodGuo; this was correlated with the differential attenuation of solar UV in the water column. CPD induction was closely related to UV-B attenuation, whereas the lower attenuation of 8-oxodGuo was more closely related to UV-A irradiance. These findings demonstrate the usefulness of these assays for assessing the relative impacts of UV-B versus UV-A.

NATURAL UV-B DEFENSE MECHANISMS

Not all the effects of solar UV-B radiation should be construed as being harmful. Many plant responses, such as the induction of phenylalanine ammonia lyase (PAL), chalcone synthase (CHS) and other enzymes involved in the formation of flavonoids and other UV-absorbing secondary compounds, provide a valuable mechanism of coping with increased plant stress (109-112). Fuglevand et al. (109) reported that UV-B, UV-A and blue light signal transduction pathways interact synergistically to regulate CHS gene expression in *Arahidopsis*. Numerous screening compounds have been found to confer UV-B protection in terrestrial plants. These include a number of flavonoids, flavonol glycosides, cinnamic acids, carotenoids and anthocyanins (110-114). Phytoplankton are known to produce UV-absorbing compounds such as mycosporine-like amino acids, which serve as protective screens (17,18,115). UV-screening compounds have also been recorded in tropical red algae (18).

Flavonoids have been shown to provide protection against solar radiation-induced DNA damage (1,46,114). They have been found to provide UV protection to guard cells in soybean, thereby playing an adaptive role in water stress regulation (116). Flavonoids have also been shown to play an important protective role against insect predators (112). Genotype differences in flavonoids and other phenolic compounds between UV-B-sensitive and UV-B-tolerant genotypes have been reported by a number of investigators (111,112). Markham et al. (117) have reported a possible protective role for 3',4'-dihydroxyflavones induced by UV-B radiation in a UV-tolerant rice cultivar, 'M202,' which appears to be unrelated to their ability to absorb radiation in the 290-320 nm region. Thus, in addition to serving as UV-screening pigments there is growing evidence that flavonoids and other phenylpropanoids perform other subtle protective roles such as free radical scavenging or improved energy dissipation (117). Ibdah et al. (118) have published action spectra for the accumulation of flavonol and betacyanin in *Mesembryanthemum crystallinum* under enhanced UV-B radiation. Wilson et al. (119) have demonstrated the importance of UV-A exposure in the UV-B-induced accumulation of specific flavonoids in *Brassica nopolux* L.

Anthocyanins are also believed to play an important role in UV-B protection, possibly because of their function as antioxidants (120,121). Anthocyanin accumulation requires light and generally coincides with periods of high excitation pressure and increased potential for photo-oxidative damage due to an imbalance among light capture, CO₂ assimilation and carbohydrate utilization (e.g. greening of developing tissues, senescence and adverse environmental conditions) (121). Steyn et al. (121) have suggested that light attenuation by anthocyanins may help to reestablish this balance and thus reduce the risk of photo-oxidative damage. They further suggest that the association between anthocyanins and oxidative stress appears to relate to the ability of anthocyanins to reduce excitation pressure and hence the potential for oxidative damage (121). As might be expected of light screens, anthocyanins generally accumulate in peripheral tissues exposed to direct light, such as the upper epidermis. They also accumulate throughout the leaf in mesophyll tissue and in trichomes.

Depending on the species and developmental stage, red, blue or UV wavelengths may play a role in anthocyanin synthesis, through mediation of phytochrome, CRY or putative UV receptors (121,122). High PAR levels are generally required for high levels of anthocyanin production (121). The UV inducibility of anthocyanins and the ability of anthocyanins to absorb UV-B radiation have led investigators to postulate a UV-B-protective role for anthocyanins, but there are still many questions that need to be answered before a general UV-protective function can be ascribed to these compounds (121).

IMPORTANCE OF SPECTRAL BALANCE ON PHOTOSYNTHETIC RESPONSES

Increased exposure to UV-B radiation has been reported to inhibit photosynthesis and photosynthetic productivity in a number of sensitive plant species (7,44,123,124). Jansen et al. (125) and Babu et al. (126) have shown the importance of spectral balance in the degradation of D1 (the herbicide-binding polypeptide of Photosystem II [PSII]) and D2 proteins in terrestrial plants. Shelly et al. (127) observed an interactive effect of PAR and UV-B on PSII electron transport in the marine alga *Dunaliella tertiolecta*. Hirose and Miyachi (128) demonstrated that reactivation of photosynthesis in the cyanobacterium *Anacystis* after UV-A exposure was stimulated by PAR, particularly wavelengths in the blue and red regions.

Murali et al. (63) reported that reductions in photosynthesis of up to 17% were obtained in greenhouse and field studies when a UV-B-sensitive soybean cultivar, 'Essex,' was subjected to biologically effective levels of UV-B radiation corresponding to a 16% ozone depletion. However, Miller et al. (129) failed to obtain any change in net carbon exchange rate when 'Essex' soybean was grown in open-top chambers in the field with UV-B irradiation provided at lower doses.

Several targets of UV-B irradiation have been identified (1,130). Photosystem I appears to be relatively resistant to UV-B exposure (7). Sites around PSII are generally considered the most sensitive to UV-B radiation (7), and elevated levels of UV-B have been shown to cause photoinhibition and photodamage

to PSII reaction centers. Baker et al. (124) have pointed out, however, that such photoinhibition and photodamage to PSII occurs only after inhibition of CO₂ assimilation characteristics. They concluded, therefore, that the primary damaging effect of UV-B on photosynthesis is not on PSII reaction centers but on a range of important soluble enzymes in the chloroplast. They further postulated that high PAR protection is conferred by some component of the Calvin cycle (e.g. ribulose 1,5-bisphosphate carboxylase [Rubisco]) rather than by the activity of UV-repair enzymes (photolyases). Under field conditions in which there may be a combination of elevated temperatures (35°C) and long periods of UV-B exposure, damage from photoinhibition and UV-B irradiation may have an additive inhibitory effect on photosynthesis in certain species (7).

Strid et al. (131) studied the effects of supplemental UV-B on *Pisum sativum* L. and concluded that supplemental UV-B with low PAR was detrimental to a number of changes in the photosynthetic apparatus in mature pea leaves. Under high PAR they obtained reduced damage under enhanced UV-B and suggested that both protective and photorepair mechanisms may be operating under high PAR. Turcsanyi and Vass (132) reported that the target for UV-A-induced inhibition of photosynthetic electron transport was the PSII complex.

IMPORTANCE OF ACTION SPECTRA FOR ASSESSING UV-B EFFECTS ON PLANTS AND NEED FOR AN IMPROVED BIOLOGICAL SPECTRAL WEIGHTING FUNCTION

Researchers have long recognized the importance of having suitable plant action spectra and biological spectral weighting functions (BSWF) for assessing the biological effects of stratospheric ozone reduction and the attendant increase in UV-B radiation on terrestrial plants (13,43,133,134). For each action spectrum a normalized sensitivity coefficient (radiation amplification factor [RAF]) can be calculated as the relative increase in biologically effective UV irradiance for a given relative decrease in the atmospheric O₃ column amount (134). Monochromatic and polychromatic approaches for obtaining action spectra have been used in both laboratory and field (43,135-140). Flint and Caldwell (138) subjected oat plants to different polychromatic combinations of UV-B and UV-A in the field and showed that both UV-B and UV-A had an inhibitory effect on stem elongation. UV-A also appeared to have a mitigating influence on UV-B inhibition.

Recent evidence obtained in UV-exclusion studies conducted at Beltsville, MD, on cucumber (*C. sativus* L.) (49) and lettuce (*Lactuca sativa* L.) (51) and in UV-exclusion experiments conducted at Raleigh, NC (139,140), indicates that the biological effects of the UV-A component of sunlight may be of much greater importance than investigators formerly believed. These findings suggest that the generalized plant weighting function developed by Caldwell (133) may not be adequate. Action spectra data obtained by Quate et al. (141) and Cooley et al. (137) support this contention.

Cooley et al. (137) obtained significant genotype differences in polychromatic UV action spectra for various growth responses between the dicotyledon *Bellis perennis* L. (daisy) and the grass *Cynosurus*

cristatus L. (crested dog's tail). The plants were grown in the natural environment, and ambient daylight was supplemented with five different UV irradiances centered at eight different wavelengths (313, 318, 320, 322, 339, 348, 356 and 377 nm). Different spectral responses were observed between the two species. *Bellis perennis* exhibited a substantial action maximum at 313 nm for the inhibition of aerial, root and total dry weight and for the inhibition of leaf expansion, but longer wavelengths were relatively ineffective on these growth parameters; in contrast, *C. cristatus* showed negligible response to 313 nm for inhibition of aerial, root and total dry weight but substantial responses to longer wavelengths, especially 339 and 348 nm. These findings have given impetus to the need to develop improved BSWF to give greater weight to wavelengths in the UV-A region of the spectrum (142,143).

Micheletti et al. (134) used a detailed radiative transfer model to calculate the dependence of the RAF on the O_3 column amount and the solar zenith angle for several commonly used action spectra. A simple mathematical model was used to interpret the results in terms of the semilogarithmic slope of the action spectra in the UV-B and UV-A wavelength ranges. They showed that the RAF may be overestimated substantially if the UV-A portion of an action spectrum is significant but is neglected (134). This was illustrated using several idealized action spectra as well as published action spectra for plant responses to UV irradiation. Madronich et al. (144) tabulated RAF for 33 different biological action spectra, using the original data as well as extrapolations to 400 nm. For seven of these spectra, extrapolation led to reductions by at least 0.2 RAF units; for other spectra, extension to 400 nm did not result in significantly different RAF values. For the new plant action spectrum proposed by Flint and Caldwell (142), extrapolation from the longest wavelength of measurements (366 nm) to 400 nm led to additional reductions of the RAF. Although such extrapolations are without physical basis, they illustrate the potential errors in RAF determinations from incomplete action spectra (134). Although further studies are needed on other plant species, initial validation studies in both laboratory and field are encouraging; the use of an improved BSWF should greatly enhance the quality of UV studies.

CONCLUSIONS

The plant's ability to cope with the damaging effects of UV radiation depends on its ability to reduce exposure (through optimization of growth and production of UV-absorbing compounds) and its ability to repair or replace damaged molecules. The protective effects of high PAR against elevated UV-B may also be indirect, by increasing leaf thickness and the concentration of flavonoids and other phenolic compounds known to be important in UV screening. The expression of these mechanisms of UV resistance is greatly influenced by spectral quality and irradiance. Action spectra indicate that wavelengths in the UV-A to blue range are most effective in repairing DNA damage. To achieve meaningful results in UV-enhancement studies, it is therefore important that a proper spectral balance be maintained in the ratio of PAR-UV-B and UV-B-UV-A radiation and that an improved BSWF be used to give greater weight to the UV-A component. Further studies are required to delineate the nature of

specific interactions of UV-A, UV-B and PAR effects in selected plants. Efforts should be made to carefully control, monitor and report each of these wavebands when conducting UV studies.

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