# Effects of UV-B Radiation on Photosynthesis

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## ABSTRACT

Several component reactions of photosynthesis, and net $CO_2$ assimilation rates have been shown to be detrimentally affected by UV-B radiation levels equal to or above those presently received at various locations on the earth's surface. Many of these studies, however, were completed under environmental conditions that deviated from ambient field conditions to such an extent that extrapolation of results for predictive purposes would probably overestimate the harmful effects of reduced atmospheric ozone levels and the concomitant increases in UV-B radiation. Nevertheless, the photosynthetic process has been shown to be sensitive to UV-B radiation and, therefore, warrants further study. The ability of plants to tolerate increased levels of UV-B radiation, relative to photosynthetic capacity, may be dictated by acclimation processes that would intensify UV-B attenuation prior to its absorbance by sensitive components or reactants of photosynthesis.

## INTRODUCTION

Experimentally increasing the quality and quantity of polychromatic ultraviolet-B (UV-B, 280-320 nm) radiation equivalent to atmospheric ozone reductions of 50% or less adversely affects various component reactions of photosynthesis and reduces carbon assimilation rates in several native and agronomically important plants. Although the underlying objective of this research has been to develop and refine predictive capabilities relative to the impact of specific increases in terrestrial UV-B radiation on plant growth, productivity, and physiological processes such as photosynthesis, this objective has yet to be achieved. This is particularly true regarding a relatively subtle increase in UV-B radiation corresponding to the projected 3 to 5% reduction in atmospheric ozone (National Academy of Sciences 1984).

Although relatively few plants have been evaluated under UV-B radiation levels corresponding to specific decreases in atmospheric ozone concentrations, a wide range in sensitivity to UV-B radiation is apparent between plant species (Caldwell et al. 1975; Biggs and Kossuth 1978), as well as within cultivars of single species (Krizek 1978; Biggs et al. 1981). Similarly, sensitivity of the component reactions of photosynthesis varies among plant species (Vu et al. 1982a) and is probably associated with differential UV-B radiation attenuation properties expressed within various

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plants (Robberecht and Caldwell 1978; Robberecht et al. 1980). Unfortunately many studies addressing the effects of UV-B radiation on carbon assimilation rates by intact plant tissues, or the component reactions of the photosynthetic apparatus, utilized very high UV-B radiation levels and/or other environmental parameters deviated considerably from those present under ambient field conditions. Thus, many studies need to be repeated with low levels of supplemented UV-B radiation corresponding to the reduction in atmospheric ozone projected to occur over the next century. Recent development of a modulated lamp system (Caldwell et al. 1983) permits UV-B radiation enhancement corresponding to specific reductions in atmospheric ozone under field conditions. Although this lamp system may not be feasible in studies such as evaluating crop productivity within large plots, every effort should be made to employ this type of lamp system in studies addressing the effects of UV-B radiation on photosynthesis.

The purpose of this chapter is to present a summary of the research that has been conducted over the past decade and contributed to the present knowledge relative to UV-B radiation effects on carbon assimilation of native and agronomically important plant species.

## CHLOROPHYLL

Low visible light intensities concomitant with UV-B radiation is a rather well documented interaction that tends to reduce plant growth and enhance damage to physiological processes (Sisson et al. 1974; Sisson and Caldwell 1976; Teramura et al. 1980; Biggs et al. 1981). Most reports of chlorophyll reduction were determined under experimental conditions where very low visible light regimes (e.g., Vu et al. 1981, 1982a) were used or with plants exposed to very high UV-B irradiance levels (e.g., Tevini et al. 1981). Vu et al. (1982a), for example, observed a 40% reduction in chlorophyll content and a 35% reduction in carotenoids when soybean plants were exposed to high doses of UV-B radiation in a greenhouse where visible light was approximately 200 μmol $m^{-2}$ $s^{-1}$ (PAR, 400-700 nm). Teramura et al. (1980), however, did not observe reduced chlorophyll concentrations within soybean plants exposed to various UV-B radiation and visible light levels (530 to 1600 μmol $m^{-2}$ $s^{-1}$ PAR). Even though chlorophyll concentrations remained similar between the UV-B radiation treated and control plants, photosynthetic rates were shown to be clearly inhibited at low visible light levels. Similarly, photosynthetic rates were shown to be depressed in pea (Pisum sativum) (Brandle et al. 1977) and Rumex patientia L. (Sisson and Caldwell 1976) exposed to moderate UV-B radiation levels. No chlorophyll reductions were noted in these studies when PAR levels were greater than 600 μmol $m^{-2}$ $s^{-1}$. An increase in chlorophyll concentration has been reported in soybean plants exposed to moderate UV-B radiation levels and 750 μmol $m^{-2}$ $s^{-1}$ PAR, and in field-grown spinach (Spinacia oleracea L.) exposed to high UV-B radiation levels (Esser 1980).

Photostability of chlorophyll appears to be somewhat species-dependent (Monfort 1950) and is readily destroyed by visible light (Shirley 1945), intense UV-C radiation at 254 nm (Cline and Salisbury 1966), and reportedly by UV-B radiation (Basiouny et al. 1978; Vu et al. 1981, 1982a). Tanada and Hendricks (1953) suggested that chlorophyll destruction by UV-C radiation is the result of a disturbance of some basic metabolic process rather than an immediate and direct destruction of chlorophyll by 254 nm radiation. This was later supported by the temperature dependent destruction of chlorophyll noted by El-Mansy and Salisbury (1971). Whether a similar effect on the biosynthesis of chlorophyll or its precursors leads to reduced chlorophyll concentrations in plant tissues exposed to UV-B radiation is not presently known. However, perhaps the initial question that warrants addressing relative to photosynthetic pigments is whether chlorophyll concentrations are altered in plants exposed to UV-B radiation levels equivalent to a reduction in atmospheric ozone of less than 20% under field conditions.



## COMPONENT REACTIONS OF PHOTOSYNTHESIS

Most research to date on the effects of UV radiation on photosynthesis has dealt with measurements of photophosphorylation, electron transport, and carbon assimilation. Early studies evaluating the effects of UV-C radiation (primarily 254 nm radiation) showed that electron transport and photophosphorylation were sensitive to this radiation. Jones and Kok (1966a,b) reported that UV-C radiation (254 nm) inhibited photoreduction of DPIP and NADP with $H_2O$ as the electron donor and that both cyclic and noncyclic photophosphorylation were inhibited. The loss of PS II activity and its associated reactions was later suggested to result from the loss of structural integrity of the lamellar membranes of the chloroplast (Mantai et al. 1970).

The disruption of chloroplast membranes by UV-B radiation has been shown to occur in soybean (Campbell 1975), Rumex patientia (Campbell et al. 1975), and pea (Brandle et al. 1977). In all these studies, damage appeared to accumulate with duration of dose. In pea, ultrastructural damage was detected after 0.25 h of UV-B radiation treatment, and 26% of the cells examined exhibited damage after 16 days treatment. The structural damage to the chloroplast lamellar membrane in this study was found to coincide with the decrease in PS II activity. However, the physical disruption that occurred may not have been the only factor causing a decrease in PS II activity since $O_2$ evolution was restored to within 12% of that of the control plants by an artificial donor (ascorbate-reduced DCPIP). Thus, UV-B radiation was suggested as an inhibitor of PS II, or some specific step in the electron transport associated with PS II apart from the resultant effects of chloroplast disruption. The latter is supported by the results of Okada et al. (1976). In this study, 254 nm radiation directly inhibited the primary photochemistry at the reaction center chlorophyll of PS II.

More recently, Noorudeen and Kulandaivelu (1982) and Iwanzik et al. (1983) showed that the impairment of photosystem II activity by UV-B radiation is due to blockage of photosystem II reaction centers rather than an inhibition of the water-splitting enzyme system. Photosystem I, on the other hand, was found to be unaffected by moderate levels of UV-B radiation in these studies. Renger et al. (in this volume) presents considerable evidence suggesting that UV radiation disrupts the plastoquinones of PS II leading to a loss of activity in the primary acceptor. Results of this study also suggest that, except for quantum efficiency, UV-B and UV-C radiation act similarly at this site.

Comparing the effects of UV-B radiation on $C_3$ and $C_4$ plants, Basiouny et al. (1978) found that of the four $C_3$ plants tested, Hill reaction activity

was significantly reduced in collards (Brassica oleracea), oats (Avena sativa), and soybeans. They reported no reductions of Hill activity in peanuts (Arachis hypogaea) ($C_3$), sorghum (Sorghum bicolor) ($C_4$), and maize (Zea mays) ($C_4$). This lower sensitivity displayed by $C_4$ plants may have been due to sclerification of tissue, nearly vertical orientation of leaves with protective based sheaths, and/or to their narrow leaves. Ultraviolet-B radiation exposure resulted in significant reductions in plant height and fresh or dry weight of the $C_3$ plants tested; no significant biomass reductions occurred in the $C_4$ plants.

Monochromatic radiation at 296 nm and 298 nm was found to inhibit RuBP carboxylase activity in tomato (Lycopersicum esculentum) and pea (Thai 1975). Recently, Vu et al. (1982a) reported significant reductions in the activity of this enzyme in soybean ($C_3$), pea ($C_3$), and tomato ($C_3$) exposed to polychromatic UV-B radiation: the reductions in RuBP carboxylase activity correlated well ($r^2 > 0.79$) with reductions in photosynthetic rates in both soybean and tomato. Activity of PEP carboxylase was significantly decreased in maize ($C_4$) exposed to the higher UV-B radiation levels while low UV-B dose rates enhanced the activity of this enzyme. Soybean and pea soluble protein levels were significantly decreased at the higher levels of UV-B radiation. These reductions were suggested to be a reflection of the RuBP carboxylase reductions noted, since this enzyme makes up a large fraction of the total leaf protein. Thus, it was suggested that UV-B radiation inhibits protein synthesis leading to the observed reductions in RuBP carboxylase activity. These results were not, however, consistent with the decrease in RuBP carboxylase and increase in soluble leaf proteins found in tomato plants exposed to UV-B radiation. In a similar study, Vu et al. (1982b) suggested that the inhibition of RuBP carboxylase activity by UV-B radiation in soybean was due mainly to protein destruction rather than inactivation.

Tevini et al. (1981) found large increases in soluble proteins in the leaves of maize, bean (Phaseolus vulgaris L.), barley (Hordeum vulgare L.), and radish (Raphanus sativus L.) exposed to very high UV-B radiation levels. Similarly, leaf protein increases were found in potato (Solanum tuberosum L.), spinach, radish, and bean exposed to moderate levels of supplemented UV-B radiation under ambient field conditions (Esser 1980). As suggested by Vu et al. (1982a), more definitive studies are needed to more clearly define the effects of UV-B radiation on soluble protein, and RuBP carboxylase and PEP carboxylase activity.

## CARBON ASSIMILATION

The effect of UV-B radiation on carbon assimilation rates has been determined for a relatively large number of agronomically important, and native plant species. With few exceptions, published research suggests that nearly all plants evaluated will be detrimentally affected, to some degree, by an increase in terrestrial UV-B radiation. As previously stated, however, many of these studies need to be repeated under ambient conditions and more subtle levels of UV-B radiation (e.g., < 20% atmospheric ozone reduction simulated). Nevertheless, the noted reductions in photosynthetic capacity of native and agronomically important crop plants may indicate a detrimental effect by an increase in terrestrial UV-B radiation levels. As such, careful experimentation is needed to explore further the potential deleterious effect, if any, and to quantify any observed reductions in the



photosynthetic capacity of plants. Of particular importance is the need to carry out any future experiments under high visible fluxes similar to or approaching ambient levels. It is well known that low visible light enhances the deleterious effects of UV-B radiation on the photosynthetic apparatus (Sisson and Caldwell 1977; Teramura et al. 1980; Teramura 1982). Low visible flux has been shown to result in thin leaves, lower chlorophyll a/b ratios, and less UV-B-absorbing pigments (Warner and Caldwell 1983). These factors, and perhaps others mediated by low visible flux levels would tend to decrease the attenuation of UV radiation prior to its absorption by the chloroplast. Thus, the net effect of low visible irradiation levels would be to increase the sensitivity of plant photosynthesizing surfaces to UV-B radiation.

Reported effects on guard cell activity, as measured by stomatal diffusion resistances, has been variable. Brandle et al. (1977) reported that moderate levels of UV-B radiation had no effect on the stomatal resistance of pea. Teramura et al. (1983), on the other hand, reported that the stomatal resistances of radish and cucumber (Cucumis sativus L.) increased; a 3-fold increase developed in cucumber for approximately 8 days, and thereafter, stomatal activity ceased. Bennett (1981) also reported a small increase in stomatal resistance in cucumber, bean, and soybean; the increases noted coincided with photosynthetic rate reductions. Because carbon assimilation is dependent upon functional guard cells of the stomata, and the diffusion of $CO_2$ to the stomatal cavity, further research seems warranted to determine the impact, if any, of UV-B radiation on guard cell activity.

Perhaps the most intriguing question being addressed relative to carbon assimilation is whether the repression of photosynthesis is dose-dependent and cumulative (i.e., whether reciprocity is maintained). A reciprocal relationship was demonstrated in component reactions of photosynthesis for isolated spinach chloroplasts exposed to UV-C radiation at 254 nm (Jones and Kok, 1966a). They suggested that UV photoinhibition was independent of oxygen and thus would not be similar to the oxygen-dependent photobleaching of chlorophyll by intense visible radiation.

Teramura et al. (1980) demonstrated reciprocity in soybeans exposed to four levels of UV-B radiation. The effect of UV-B radiation was more efficient in reducing photosynthetic rates when plants were exposed to concomitant low visible radiation. Even UV-B irradiance corresponding to ambient levels reduced photosynthesis when PAR intensities were low (528 $\mu E\ m^{-2}\ s^{-1}$ PAR). Trocine et al. (1981) also demonstrated that reciprocity occurred in the photosynthetic inhibition of two of three seagrasses. The differential degree of UV-B sensitivity within these species was suggested to be a function of epidermal cell wall thickness and the associated transmittance properties. Stimulated synthesis of anthocyanin and other flavonoid UV-B radiation-absorbing pigments was also evident in the plants exposed to UV-B radiation.

Reciprocity has also been demonstrated in R. patientia exposed to four levels of UV-B radiation (Sisson and Caldwell 1977). The reciprocal relationship shown in this plant, however, may have partially resulted through a gradual deterioration of the epidermis (Robberecht and Caldwell 1978), thereby increasing the transmittance of UV-B radiation to the sites of the component reactions of photosynthesis during leaf ontogeny. Reductions in photosynthesis were especially evident during the early stages of leaf

ontogenesis, and leaf longevity was reduced by increased UV-B radiation levels. However, leaf growth did not display a reciprocal relationship to UV-B radiation, but was found to be dependent upon dose rate and was affected primarily during the early state of leaf ontogeny (Sisson and Caldwell 1976, 1977). In a similar experiment using Cucurbita pepo, photosynthesis was repressed in a cumulative manner in fully expanded leaves but not through leaf ontogenesis (Sisson 1981). Although absorbance of UV-B radiation by extracted pigments (flavonoids and other UV-B radiation-absorbing pigments) increased substantially, UV-B radiation attenuation was apparently insufficient to protect completely the photosynthetic apparatus or leaf growth process.

## ACCLIMATION

The ability of plants to acclimate to increased levels of terrestrial UV-B radiation provides one possible avenue for plants to tolerate this radiation without a decrease in productivity or displacement by a more resistant plant. As pointed out by Caldwell (1981), if acclimation results from a phenotypic response already available to plants, the rate of UV-B radiation increases over time may be of little consequence. If, on the other hand, this acclimation process involves a change in genetic composition that may involve considerable time to evolve, then the rate of UV-B radiation increase may be of considerable importance. That plants do possess the ability to acclimate to the UV-B environment was amply supported by a study conducted by Bogenrieder and Klein (1977). They exposed Rumex alpinus seedlings to ambient irradiance after being grown in an environment free of UV-B radiation. The seedlings displayed severely depressed photosynthetic rates and some plants were killed after a 3-day exposure period. Thus, plants are apparently tolerating ambient levels of UV-B irradiance by acclimation processes induced by environmental stimuli that include UV radiation. Although plants appear to possess mechanisms by which they can respond to environmental stimuli and acclimate to changes in radiation, neither the rates nor limits of acclimation are known for any plant. The result of such acclimation will probably determine whether or not any one plant species will be deleteriously affected. Since plants are known to possess a wide range of sensitivities to UV-B radiation, morphological and biochemical responses to increased levels of ambient UV-B radiation might be species dependent. Alternatively, if even sensitive plants possess the capacity to acclimate to small increases in UV-B radiation, the resultant effects may be nonexistent.

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