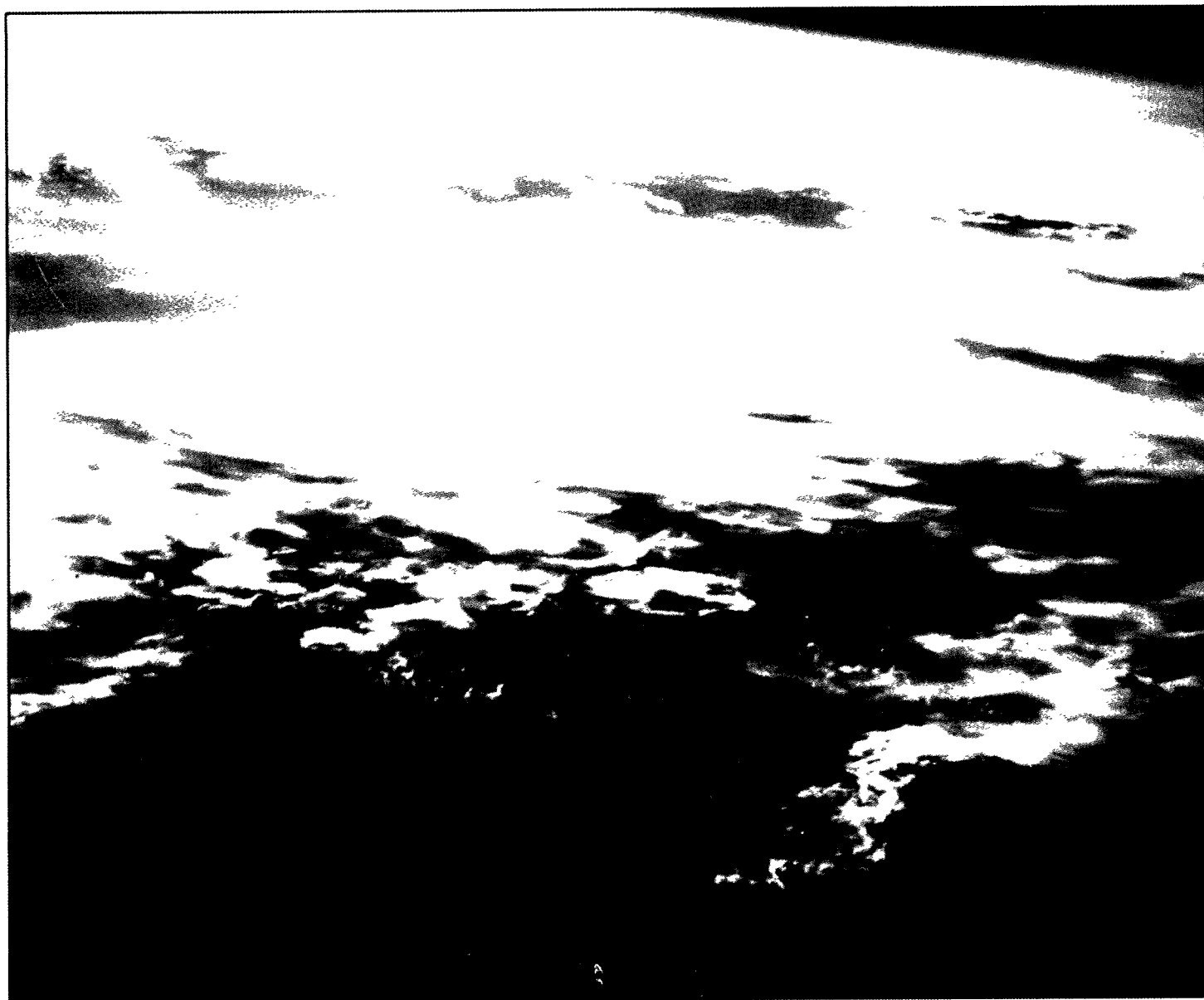




# Assessing the Risks of Trace Gases That Can Modify the Stratosphere

Volume VIII:  
Technical Support Documentation  
Ozone Depletion And Plants



# **Current Risks and Uncertainties of Stratospheric Ozone Depletion Upon Plants**

**Volume VIII**

**Technical Support Documentation for Assessing  
the Risks of Trace Gases That Can Modify the  
Stratosphere**

**December 1987**

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#### ACKNOWLEDGEMENTS

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## PREFACE

Since the discovery of ultraviolet radiation by J.W. Ritter in 1801, the ecological consequences of solar UV has only recently come to the forefront of public attention due to possible stratospheric ozone depletion resulting from anthropogenic pollutants. Although during the past decade our knowledge of the effects of UV-B radiation has grown prodigiously, we still lack sufficient information for realistic appraisals of risks and uncertainties. This is principally due to an absence of standardization in experimental procedures and the paucity or virtual void of research in key areas. The data we do possess, however, provide a rough basis for understanding some consequences of enhanced solar UV radiation. On this premise, I have evaluated the possible risks and uncertainties concerning stratospheric ozone depletion and its impact on plants.

The first section addresses the risk to crop yield resulting from both direct and indirect effects of enhanced solar UV-B radiation. In the second section, the uncertainties associated with the effectiveness of UV-B radiation are presented, and the last section deals with recommendations for standardization of experimental procedures and future research priorities.

I thank Ms. Joan Jeschelnik of the Department of Botany, University of Maryland, and ICF Incorporated, Washington, D.C., for their excellent assistance in typing this manuscript and to Drs. Martyn Caldwell, N.S. Murali, and John Hoffman for their suggestions in the organization of this work.

I would very much appreciate receiving any comments or suggestions to make this report an accurate and complete assessment of our current state of knowledge.

Alan H. Teramura  
College Park, Maryland  
October 25, 1984

## 1. INTRODUCTION

In terms of biological response, ultraviolet (UV) radiation spans a considerable portion of the electromagnetic spectrum. Therefore for convenience, it has arbitrarily been partitioned into three wavebands. The shortest waveband (UV-C) extends between 200-280 nm and is well known for its germicidal effects. The middle UV region (UV-B) contains radiation between 280-320 nm and produces erythema or sunburn in humans. The longest waveband is UV-A, which includes radiation from 320-400 nm. Although not visible to the human eye, UV-A radiation is important to insect vision. All three are natural components of the solar spectrum; however, due to the large absorption by the earth's atmosphere, most of this radiation is greatly attenuated prior to reaching the earth's surface. The primary attenuator of UV radiation is stratospheric ozone, which efficiently absorbs nearly all wavelengths shorter than 290 nm. Therefore, only the UV-B and UV-A wavebands naturally occur at the earth's surface. Since UV-B radiation contains much more energy than UV-A, it has extremely important biological consequences.

The protective ozone layer is located at an altitude of between 15 and 40 km in the stratosphere and periodically undergoes natural variations in concentration, which results in substantial fluctuations in UV reaching the earth's surface. For example, ozone concentrations may vary as much as 30% within the continental United States along latitudinal gradients. Furthermore, ozone concentrations vary temporally, such as with the passage of regional weather systems, as well as seasonally and annually. In addition to these natural variations, recent attention has focused primarily upon changes in ozone concentration resulting from man-made atmospheric pollutants (NAS 1979, 1984; NRC 1982). Presently, there are some 50 molecular species involved in over 150 chemical reactions known to involve ozone. Thus, our current concentration of stratospheric ozone depends upon a dynamic balance between chemical reactions that create and destroy ozone (see Appendix B, Stratospheric Chemistry and the Nature of Ozone). Increasing releases of these chemical pollutants tend to favor ozone destruction and reduce stratospheric ozone concentrations, thereby allowing more UV to penetrate to the earth's surface. For example, the photodissociation of chlorofluoromethane (CFM), principally from spray propellants, refrigerants, and foam-blowing agents, contributes a substantial chloride ( $\text{ClO}_x$ ) source. CFMs are so inert in the lower atmosphere that they are not readily removed by the normal atmospheric cleansing action of precipitation. Instead, they slowly migrate into the upper stratosphere where they eventually become photodissociated by high energy radiation, releasing free chlorine atoms. Once they reach the stratosphere, these and other chemicals have a long residence time during which they participate in catalytic reactions that destroy ozone. For example, each chlorine atom at 30 km destroys an average of 10,000 ozone molecules. Since stratospheric dynamics are so slow, there is a century lag between the time these compounds are released at ground level until the period when equilibrium ozone reductions become established. Therefore, those atmospheric pollutants being released now, will continue to affect stratospheric ozone concentrations for the next 100 years.

This report examines all of the published and unpublished material currently available to assess the likely impact of projected increases in UV-B radiation upon global crop productivity and the distribution and abundance of

plants in natural ecosystems. The limitations to this assessment are formidable, particularly due to a paucity of experimental data and the slow development of appropriate technology. Therefore actual risks may be far greater or somewhat less than current knowledge indicates.

## **2. ISSUES AND UNCERTAINTIES IN ASSESSING THE EFFECTS OF UV-B RADIATION ON PLANTS**

In assessing the impacts of a potential increase in global UV-B radiation on plants, experiments ideally should be designed to develop a data base that perfectly simulates future conditions for all plant species. Such idealized experimental designs should include all direct effects in addition to all the possible significant combinations of effects (interactions). For example, it is projected that in addition to increases in the level of UV-B radiation, atmospheric levels of CO<sub>2</sub> (carbon dioxide) will also sharply rise during the next century. Therefore, experiments should examine both effects independently, as well as the product of their interaction. Of course, one also needs to know how these would change under conditions of drought, mineral deficiency, etc. After such a perfect simulation, accounting for all possible occurrences, it would not be difficult to assess the potential impacts of global UV-B radiation increases with high precision. Unfortunately, such ideal circumstances rarely, if ever, occur. In reality, we must make assessments based upon imperfect experimental designs, with only very selective and sometimes unrealistic growing conditions, and based on only a few representative plant species. Therefore, our existing data base for this assessment can lead only to possible, not conclusive, scenarios.

### **2.A. Issues concerning UV dose and current action spectra for UV-B impact assessment**

Total global UV-B irradiance is dependent on a number of factors, including solar angle, latitude and altitude, stratospheric ozone concentration, atmospheric turbidity, and degree of cloud cover. Additionally, the earth-sun distance and minor solar fluctuations also contribute to annual variations in irradiance (Caldwell 1971). Because of diurnal and seasonal variations in many of these factors, the spectral composition of solar radiation also varies substantially. Solar UV-B irradiance varies diurnally, peaking at solar noon. Annually, UV-B irradiance is maximum during summer and minimum during winter. Experiments evaluating the effectiveness of UV-B radiation on plants typically do not account for such changes because of practical difficulties in monitoring and supplementing UV-B radiation. Generally, supplemental UV-B radiation is provided using filtered sunlamps as a squarewave function by using timers. Such a system provides a proportionately greater UV irradiance during morning and late afternoons than would be anticipated outdoors. Furthermore, supplemental radiation is provided even during cloudy and overcast skies, when the level of ambient UV-B may be less than 50% of clear sky irradiances due to the absence of the direct beam component. Thus, supplemental UV-B radiation provided by investigators in most studies is an unrealistic simulation of the natural patterns of solar UV radiation. Caldwell et al. (1983) have designed a modulated system to monitor ambient UV-B and provide the desired supplemental UV-B dose. This system provides a more realistic simulation of anticipated ozone depletion, since it modulates lamp output in accordance with actual

levels of incoming solar UV radiation. Because of the cost of installation, it has not been widely adopted (see Section 5, Recommendations).

Another major limitation with most UV-B studies is that the UV-B dose is based upon the concentration of ozone during the summer solstice or other specific day with a fixed ozone depletion. In reality, ozone concentrations are highly variable, being maximum in the late winter and early spring and minimum during late summer and autumn. Since a fixed ozone reduction will result in large differences in UV irradiances during different seasons, the assumption of a fixed level of ozone depletion further adds uncertainty in the evaluation of UV-B dose.

Photon absorption is the primary event in a biological response to radiation. Since photon absorption is a resonance phenomenon, its probability is strongly wavelength dependent; hence, the effectiveness of radiation in producing a biological response will also be wavelength dependent. The relative effectiveness of UV radiation for a given biological response can be expressed using a function  $E(\lambda)$ , normalized to unity at the most effective wavelength. Such a function is known as the action spectrum for the given biological response. Action spectra are essential for 1) comparing the biological effectiveness produced by sources with different spectral irradiance, 2) evaluating the relative increase of solar UV radiation due to possible stratospheric ozone depletion, and 3) evaluating the present natural gradients of solar UV irradiance on the earth. A brief description of these points is presented below with more specific details given in Appendix A (Action Spectra and their Key Role in Assessing Biological Consequences of Solar UV-B Radiation Change).

The source of UV-B radiation most commonly used in plant effects research is the fluorescent sunlamp, which emits radiation principally in the UV-B region. This sunlamp is a low-pressure mercury vapor lamp containing a phosphor that fluoresces primarily in the UV-B region, and emits some UV-C and UV-A radiation. Although the energy emitted comes principally from the fluorescing phosphor, some emission from mercury vapor is superimposed upon this, producing distinct lines in the spectrum. The spectral energy distribution emitted from various types of lamps varies considerably. Therefore, to compare different lamps for biological effectiveness, a weighting function is absolutely essential. This can be illustrated using two hypothetical sources, A and B, with a spectral irradiance in the range 280-300 nm and 300-320 nm, respectively (see Figure 1). The total unweighted irradiance, which is the area under each line, is identical and equal to 100 for the two sources. Line C represents an assumed biological action spectrum. The biologically effective irradiance ( $I_{BE}$ ) is given by the following relationship:

$$I_{BE} = \int I_{\lambda} E_{\lambda} d\lambda$$

where  $I_{\lambda}$  is the lamp spectral irradiance, and  $E_{\lambda}$  is the relative effectiveness of the energy to produce a response at wavelength  $\lambda$ . Thus, the biologically effective irradiance is the product of the action spectrum and the spectral irradiance at each wavelength. The weighted spectral irradiance for the two sources are shown in curves D and E: for source A and B the effective irradiances are 83.3 and 16.7, respectively. This illustrates the point that



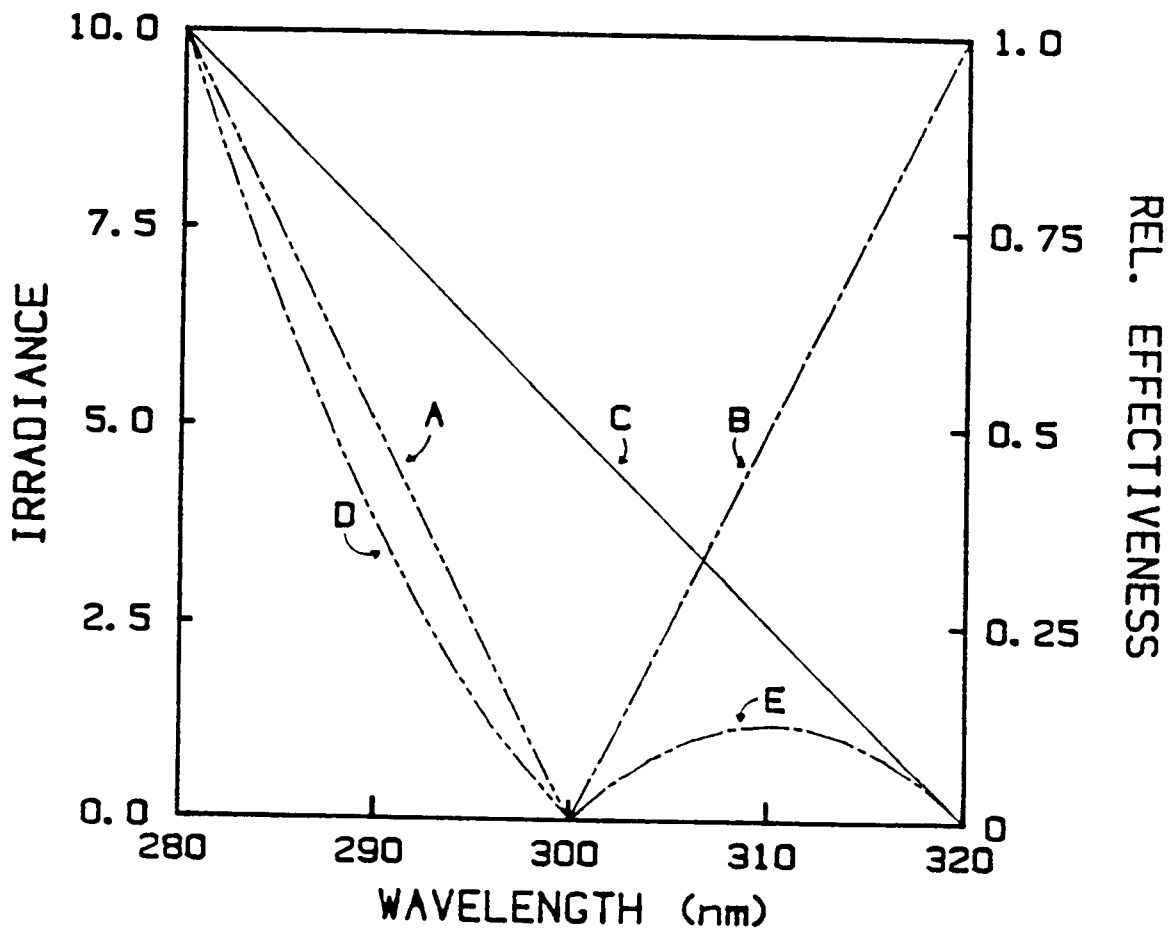


Fig. 1. Two hypothetical sources, A and B, were weighted with action spectrum C, resulting in a five-fold difference in the integrated weighted irradiance (area under curves D and E).

although the two sources have the same total unweighted irradiance, their biological effectiveness differs by five-fold.

Several UV action spectra have been developed using monochromatic radiation (Figure 2). All these share the common feature of decreasing effectiveness as wavelength increases but have considerable variation in the rate of this decrease. Most of the published UV action spectra to date were determined with isolated organelles, membranes, microorganisms, etc., rather than with intact higher plants. Caldwell (1971) has developed a generalized plant damage spectrum based upon the combined responses of a number of different plant species. The effects of UV-B radiation on a specific characteristic in an isolated organelle can differ considerably from an intact plant due to cellular shielding effects in the plant and inherent repair mechanisms. For instance, it is now well documented that the effects of UV-B radiation can be altered by visible radiation. UV-B radiation has a greater damaging effect under low levels of visible radiation than under high levels (Teramura et al. 1980; Mirecki and Teramura 1984; Warner and Caldwell 1983). Thus, an action spectrum developed on intact plants under polychromatic radiation would be preferable, and enable a more realistic assessment of the biologically effective increases in solar UV-B radiation. Caldwell et al. (1986) have recently attempted to develop such an action spectrum, and although there are experimental limitations, they were able show that it is technologically possible.

Another essential reason for developing appropriate action spectra is for the evaluation of radiation amplification factors (RAF), i.e., the relative increase in biologically effective UV-B radiation associated with a specific ozone reduction. RAF is a complex function taking initial ozone layer thickness, percent ozone layer reduction, latitude, season, and biological weighting function into consideration (NAS 1979). The increase in solar UV-B radiation as a result of ozone reduction becomes appropriate only when the biological effectiveness of this radiation is known. Without calculating an RAF, the absolute increase of total solar UV-B radiation resulting from even an appreciable ozone reduction is so small that it is insignificant. RAF values for a 16% ozone reduction at three latitudes during the time of maximum solar radiation (summer solstice for temperate and polar latitudes) are presented in Table 1. For the same change in ozone concentration, the increase in biologically effective UV-B radiation is significantly greater at higher than at lower latitudes. Table 1 additionally illustrates that RAF also varies with different action spectra.

Since solar spectral irradiance increases by orders of magnitude with increasing wavelength in the UV-B region, the tails of the action spectra have a profound effect on the net RAF. Figure 3 shows the calculated RAF values for different ozone column thicknesses according to various action spectra. The RAF values are much higher for those with steeper slopes than for those shallow slopes. Thus, the computed biological effectiveness of solar radiation could either be underestimated or overestimated if the action spectra are not realistic of true plant responses.

There is a natural latitudinal gradient of solar UV-B radiation due to differences in the prevailing solar angle and total ozone column thickness (Caldwell 1981, Caldwell et al. 1980). Such a natural gradient in UV-B

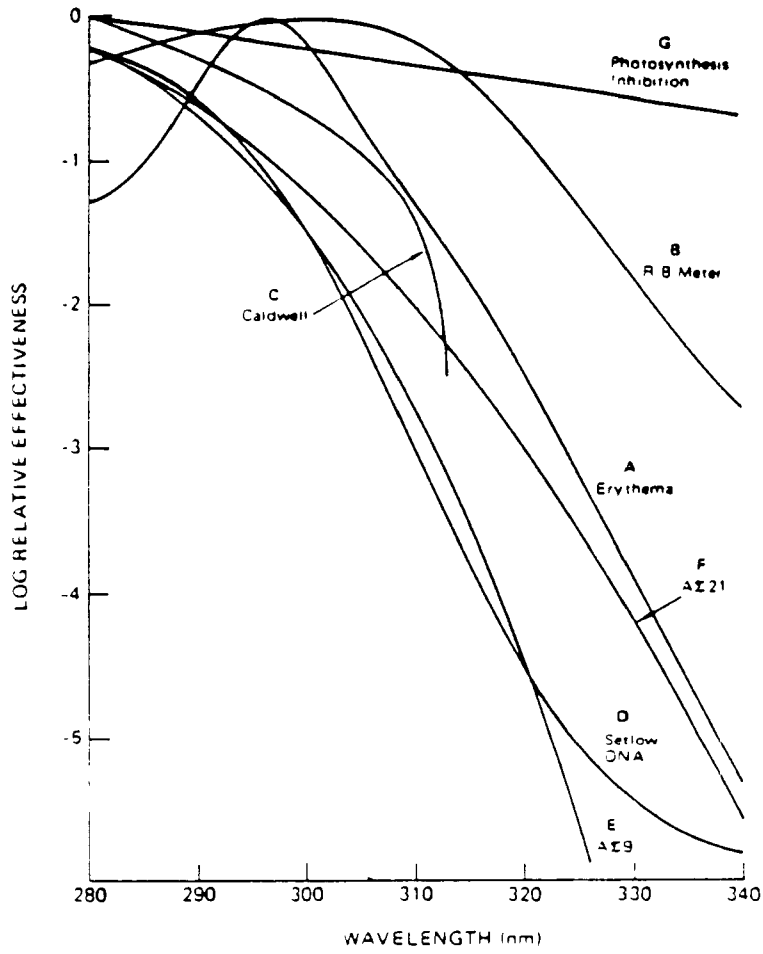


Fig. 2. Weighting functions in current use for biological UV effects.  
(NAS 1979)

**Table 1. Comparison of RAFs Calculated from Three Different Action Spectra for a 16% Ozone Depletion (from Caldwell 1981)**

Latitude	Setlow (1974)	Caldwell (1971)	Jones and Kok (1966)
20°	46.3	32.0	2.2
40°	47.5	35.0	2.3
70°	49.4	44.0	2.3

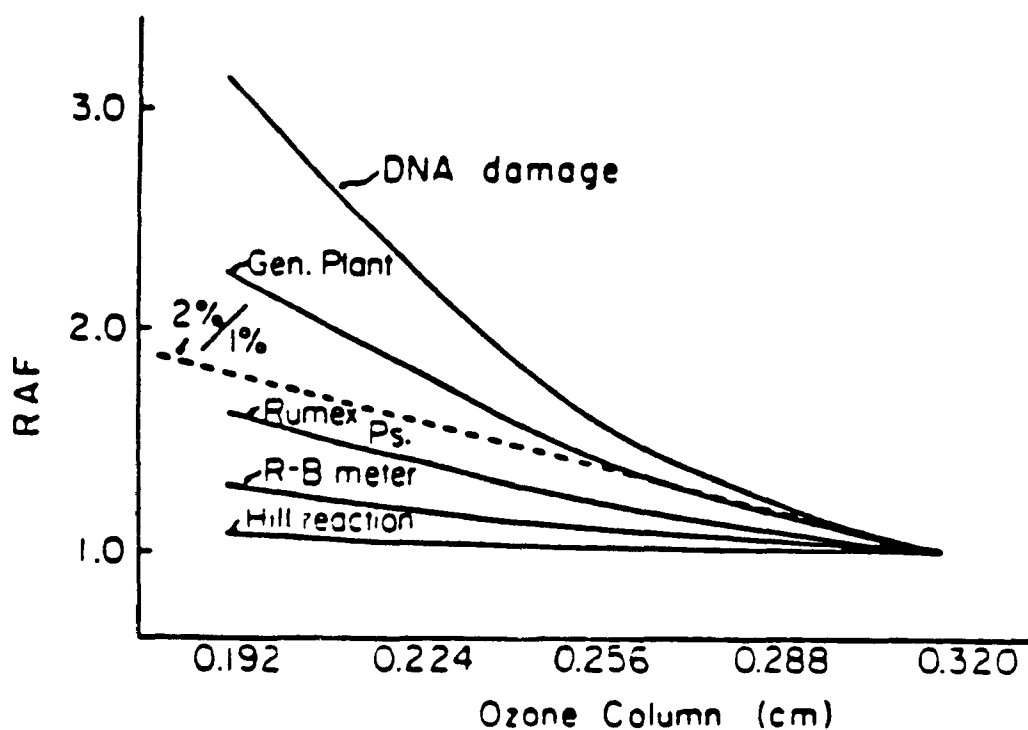


Fig. 3. Radiation amplification factors calculated for different ozone column thickness, relative to 0.32 cm, and a solar angle from the zenith of  $33.6^\circ$  calculated according to the action spectra shown in Fig. 2. The dashed line represents a case of 2% increase in biologically effective radiation for a 1% decrease of ozone. The model of Green et al. (1980) was used to calculate the solar spectral irradiance (direct beam + diffuse) used for those RAF values (from Caldwell et al. 1986)

radiation provides an opportunity to study plant responses to enhanced levels of solar UV-B radiation. Correlations between this latitudinal UV gradient and skin cancer have been used to calculate future increases of human skin cancer anticipated from a given ozone reduction (NAS 1984). Such correlations between latitude and plant responses are more difficult to make due to gross climatic and edaphic variations. However, growth chamber studies with species from different latitudes can provide some limited information. The steepness of the latitudinal gradient of solar UV-B irradiance depends upon the action spectrum used. If the spectrum has a shallow slope, there will effectively be only a very small latitudinal solar UV-B gradient, while a steep slope will show a wide latitudinal gradient.

It is evident from the above discussion that a more realistic action spectrum is needed for a proper assessment of the possible consequences of enhanced UV-B radiation due to ozone depletion. An under- or overestimation of UV-B effectiveness would result if inappropriate action spectra are used.

## **2.B. Issues concerning natural plant adaptations to UV**

There exists tremendous variability in plant species sensitivity to UV-B radiation (Krizek 1978, Van et al. 1976, Hashimoto and Tajima 1980, Tevini et al. 1981 and 1982, Tevini and Iwanzik 1982, Teramura 1983). Some species show sensitivity to current day ambient levels of UV-B radiation (Teramura et al. 1980, Bogenrieder and Klein 1978, Sisson and Caldwell 1976) while others are apparently unaffected by rather massive UV enhancements (Becwar et al. 1982, Ambler et al. 1978). Confusing this issue further are reports of equally large response differences among cultivars within a species (Biggs et al. 1981, Dumpert and Boscher 1982, Murali and Teramura 1986a,b, Murali et al. 1986). At present, the basis or mechanisms responsible for these inherent species and cultivar differences have not been well documented. For example, earlier investigators speculated that the apparent difference frequently observed between monocotyledonous and dicotyledonous plants may be due to differences in plant growth form (Van and Garrard 1975). Grasses have erect leaves while most herbaceous species generally have horizontally displayed leaves. More recently, however, Caldwell (1981, 1982) has concluded from computer simulation studies that leaf orientation probably has little effectiveness in UV avoidance due to the high proportion of the diffuse component in the global UV-B radiation flux.

There are apparently at least three main categories of natural UV protective mechanisms (Beggs et al. 1986), which may explain in part the great range of species response differences. The first includes mechanisms whereby UV-induced damage is repaired. Photoreactivation is a light-activated (UV-A and blue light primarily), enzyme-mediated process whereby pyrimidine dimers produced as a consequence of UV absorption by DNA are split (Rupert 1984). Although this has not yet specifically been demonstrated in plant tissues, numerous examples of indirect evidence exist (Beggs et al. 1986, Tanada and Hendricks 1953, Bridge and Klarman 1973), suggesting that it is a widespread phenomenon in plants. Excision repair is the process whereby potentially deleterious photoproducts of UV absorption are removed and replaced by new, correct DNA sequences. This has clearly been documented in plant tissues (Howland et al. 1975, Soyfer 1983) and is also a widespread phenomenon in animals. Postreplication repair involves the replication and combination of

intact DNA strands in exchange for damaged ones, but is yet unknown in plant tissues. Finally, quenching and free radical scavenging of oxygen singlets produced by photo-oxidation may be a means of alleviating some types of UV-induced damage. The importance and extent of these processes in alleviating UV damage in plants has not yet been well documented.

The second category of protective mechanisms are those that tend to minimize the damaging effects of UV-B radiation (Beggs et al. 1986). Probably the most important of these mechanisms in plants is growth delay. If cell division stops or is slowed upon UV irradiation, then the other repair mechanisms alluded to above could come into play and help to ameliorate the damage before it became lethal to the plant. Although many plants show a growth inhibition upon UV-B radiation exposure (for example, see Teramura 1983), it is not clear whether this inhibition is the direct effect of the damage done to the plant, or due to the activation of this protective mechanism. For example, Dickson and Caldwell (1978) found that UV-B radiation altered the pattern of cell division early in the ontogeny of *Rumex patientia*. Specifically, cell expansion was unaffected and it was the rate and not the duration of cell division that was affected. Despite these changes, *Rumex* appears to be a plant that is highly sensitive to UV-B radiation-induced damage (Sisson and Caldwell 1976, 1977).

The third category of protective mechanisms involves those that effectively reduce the amount of UV radiation actually reaching sensitive plant targets. These mechanisms include structural attenuation by the cuticle and cell wall, which seem to play only a minor role since they offer little UV absorption (Caldwell et al. 1983a, Steinhilber and Tevini 1985). The principal mechanism in this category is probably the selective absorption of UV radiation by pigments located in outer tissue layers. The most attractive biochemical candidates appear to be flavonoids and other related phenolic compounds that occur in the vacuoles of epidermal cells and have high UV absorption coefficients but are nearly transparent in the visible region of the spectrum (Caldwell et al. 1983). A large number of investigators have shown that flavonoid concentrations in plant leaves substantially increase upon UV exposure (Wellman 1982, Murali and Teramura 1985a and 1986a, Robberecht and Caldwell 1978, Tevini et al. 1981 and 1983, Flint et al. 1985). However, it has not been established how many plant species increase leaf flavonoid biosynthesis in response to increasing levels of UV-B radiation, nor whether such an increase is sufficient to completely attenuate the damaging effects of UV radiation. Some studies suggest that despite a large increase in flavonoid concentration produced in leaves, UV-sensitive targets, such as the photosynthetic machinery contained in chloroplasts, are still adversely affected (Sisson 1981, Teramura et al. 1984a, Mirecki and Teramura 1984).

Although much of the attention concerning natural plant adaptations to enhanced levels of UV-B radiation has been recently focused upon UV attenuation by flavonoids, knowledge of total leaf flavonoid concentrations alone do not account for the range of responses observed in species sensitivity. For example, total leaf flavonoid levels found in UV-B irradiated soybeans were less than those found in cucumber given the same UV-B dose, yet cucumber was found to be much more sensitive to UV (Murali and Teramura 1986a,c). Therefore, the inherent range of plant species sensitivity to UV-B radiation is probably the product of a number of UV-protective

mechanisms acting in concert within the plant. We currently need more specific information concerning plant adaptations to UV-B radiation before we can further refine our estimates of the ability of natural plant protective mechanisms to compensate for the projected increases in solar UV-B radiation.

### **2.C. Issues associated with the extrapolation of data from controlled environments into the field**

By far, the bulk of our understanding of the impacts of UV-B radiation comes from studies conducted in artificially controlled environments (Teramura 1983). Because environmental conditions within growth chambers or greenhouses are unlike those found in nature, plant responses under such conditions may neither quantitatively nor qualitatively resemble field responses. For instance, it is now widely known that plants grown in growth chambers appear to be more sensitive to a given UV dose than field-grown plants (Caldwell 1981, Bennett 1981, Teramura 1982a, Mirecki and Teramura 1984). The basis for this difference in sensitivity comes from the fact that in artificial environments (growth chambers and greenhouses) a single factor is generally manipulated, while all other factors are either kept constant or are optimized for growth. Such single-factor stresses are rarely experienced by plants outdoors. Instead, under actual conditions, plants would commonly experience simultaneous, multiple stresses. For example, plants receive their maximum daily UV-B irradiance during the period of maximum air temperatures and evaporative demand for water. Furthermore, unlike plants in growth chambers where nutrient solutions may be applied daily, most native crops and many agricultural crops grow in soils that are low or deficient in nutrients. In addition to these differences in physical factors, artificial environments almost always exclude biotic factors, such as the interactions between other plants, insects, diseases, etc.

Weighed against these shortcomings of controlled-environment studies are the enormous complexities associated with field studies. Here, daily fluctuations in environmental factors are superimposed upon longer-scale seasonal and annual fluctuations making interpretation extremely difficult and necessitating multiyear experimental designs. Both temporal and spatial variability often result in inconsistencies in plant responses between one year and the next (for examples see Biggs et al. 1984, Gold and Caldwell 1983, Teramura 1981, Lydon et al. 1986).

One potentially useful approach in attempting to understand the effects of UV-B radiation on plants under more realistic conditions has been the study of the interactions between UV and other, commonly experienced plant stresses such as water stress, nutrient deficiency, and low visible light stress (Table 2). As such, these studies are not attempts simply to mimic field conditions under artificial environments. Instead, they were expressly designed to test specific factor interactions to develop a better understanding of the effects of UV-B radiation on plants.

Currently, five studies have assessed the combined effects of water stress and UV-B radiation on plants. In the first two (Teramura et al. 1983 and Tevini et al. 1983), cucumber and radish seedlings were grown in a factorial combination of two UV-B irradiances and three levels of water stress. These studies revealed that exposure to enhanced levels of UV radiation may affect the



**Table 2. Studies Examining the Interaction Between UV-B Radiation and Other Environmental Stresses**

UV-B Radiation and Water Stress	UV-B Radiation and Mineral Deficiency	UV-B Radiation and Low PPFD*
Teramura et al. 1983	Bogenrieder and Doute 1982	Bartholic et al. 1975
Tevini et al. 1983	Murali and Teramura 1985a	Van et al. 1976
Teramura et al. 1984a	Murali and Teramura 1985b	Sisson and Caldwell 1976
Teramura et al. 1984b		Teramura 1980
Murali and Teramura, 1986c		Teramura et al. 1980
		Warner and Caldwell 1983
		Mirecki and Teramura 1984

\*PPFD = Photosynthetic Photon Flux Density

susceptibility of some crops, like cucumber, to water stress. Furthermore, water stress appeared to alter the sensitivity of radish to UV radiation by inducing flavonoid (UV-absorbing pigments) biosynthesis. Two studies (Teramura et al. 1984a and Teramura et al. 1984b) examined the effects of UV irradiation on the photosynthetic recovery from water stress and on the various components of internal water relations in soybean. Plants were grown in greenhouses under two levels of UV-B radiation and two watering prehistories (water-stressed and well-watered). The results from these studies indicated that UV-B radiation and water stress produced an additive, deleterious effect on photosynthesis. Therefore, this combination of stresses was more deleterious than either stress alone. At present, the mechanism responsible for this effect is unknown, since UV radiation had no effect on the internal water relations of soybean (Teramura et al. 1984b).

The most recent study (Murali and Teramura 1986c) assessed the effects of mild water stress and UV-B enhancement under field conditions. The results revealed no additional deleterious effects of UV-B radiation when combined with water stress. It was hypothesized that changes in leaf anatomy, increased flavonoid production, and reduced growth induced by water stress masked the effects of increased levels of UV-B radiation.

To date, three studies have focused on the interactions between UV-B and mineral deficiency. Bogenrieder and Doute (1982) compared the effects of UV-B on the growth and photosynthesis of lettuce (*Lactuca sativa*) and alpine sorrel (*Rumex alpinus*) grown hydroponically under four mineral concentrations. They concluded that plant productivity (accumulation of dry matter) became more sensitive to UV-B radiation as total mineral supply decreased. Murali and Teramura (1985a,b) hydroponically grew soybean in four levels of phosphorous (P) under two levels of UV-B radiation. Surprisingly, they found that on a relative basis, plant sensitivity (dry weight basis) to UV-B radiation decreased as P level decreased. This suggests that the greatest impact of UV-B enhancement might appear in well-fertilized (agricultural) regions, rather than in areas of low fertility. This unexpected response was at least partly due to an increase in the production of UV-absorbing pigments in the leaves of nutrient-deficient plants.

One of the most obvious differences between growth chamber and field environments is the level of visible radiation available to the plants during growth. Since most growth chambers supply visible radiation using a combination of incandescent and fluorescent lamps, visible irradiances are typically quite low, usually ranging from 10% to 40% of average midday irradiances. The concern over this difference stems from the knowledge that many of the deleterious effects of UV radiation may be ameliorated by exposures to longer wavelengths. If this is the case, then experiments conducted in such growth chambers would substantially overestimate the impact of UV effectiveness in the field. At least seven studies have addressed this question and the german conclusions of each are summarized in Table 3. Despite the fact that these data include a wide diversity of plant species and growth conditions, a clear trend emerges: plants grown in higher levels of visible radiation, more closely approximating field conditions, are less sensitive to the deleterious effects of UV-B radiation. A corollary to this conclusion is that plant sensitivity to UV-B radiation is strongly influenced by the level of visible

Table 3. Percentage Change from Mylar Controls for Photosynthesis or Growth by UV-B Radiation at Different Photosynthetic Photon Flux Densities (PPFDs).

Values in Parentheses are Changes Resulting from Concomitant PPFDs

Species	Peak PPFD ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )							Reference
	2000	1600	1400	800- 900	400- 500	200	70	
<i>Phaseolus vulgaris</i> L.	+5							Bartholic et al 1975
<i>Zea mays</i> L.	+7			+5	-8			Bartholic et al 1975
						-16		Van et al 1980
<i>Lycopersicon esculentum</i> L.	-22			+12	-24			Bartholic et al 1975
						-33		Van et al 1980
<i>Pisum sativum</i> L.					+4	-33		Bartholic et al 1975
				-19		-35		Van et al 1980
<i>Glycine max</i> (L.) Merr.		-6	-18	-58	-23			Teramura et al 1980
		-14	-29	-65	-59	-52		Teramura 1980
			0	-20				Merecki and Teramura 1984
			0	(-20)				Merecki and Teramura 1984
				-5			-25	Warner and Caldwell 1983
				(-17)			(-10)	Warner and Caldwell 1983
<i>Brassica oleracea</i> var. <i>capitata</i> L.				-6		-33		Van et al 1980
<i>Brassica oleracea</i> var. <i>acephala</i> L.				-10		-27		Van et al 1980
<i>Avena sativa</i> L.				-5		-24		Van et al 1980
<i>Rumex patientia</i> L.	-38			-30	-38			Sisson and Caldwell 1976

radiation available during growth and development, and that shaded environments maximize this sensitivity.

Two studies (Lydon et al. 1986 and Teramura and Murali 1986) have specifically examined the differences in UV-B radiation response between field- and greenhouse-grown soybean. Six soybean cultivars were grown in an unshaded greenhouse under either no UV-B radiation or a level simulating a 16% ozone depletion (at College Park, Maryland, 39°N) during the summer solstice based upon the generalized plant weighting function (Caldwell 1971). These same cultivars were also grown in the field and received either ambient levels of UV-B or levels simulating a 16% ozone depletion. In both cases, supplemental UV was applied via cellulose-acetate-filtered FS-40 sunlamps. Cultivar sensitivity ranking was based upon a combined plant response that included changes in total plant dry weight, leaf area, and plant height. A summary of those data is presented in Table 4. Taken as a whole, the relative ranking for UV-B sensitivity based on vegetative growth observed in the greenhouse was quite similar to that found in the field. The major difference was that UV-B radiation produced a substantially larger (between a two- and ten-fold) effect on greenhouse-grown plants compared with field-grown plants. However, in specific instances, quite different conclusions could be drawn from the individual data sets. For example, cultivar James might be considered rather sensitive, while York was resistant to UV-B radiation based upon experimental greenhouse data. In the field, however, these cultivars demonstrated the opposite response. Therefore, if controlled environment-to-field extrapolations are necessary, they must be done with the utmost caution. At best, general trends may be implied, but specific or quantitative extrapolations do not yet seem plausible. Part of the reason for qualitative and quantitative differences between controlled environment and field responses to enhanced levels of UV radiation may be due to confounding factor interactions about which we still have relatively little information.

#### **2.D. Uncertainties associated with crop breeding as a means of limiting UV-B impacts**

Table 5 is a summary of reports that have specifically examined the effects of UV-B radiation on numerous crop cultivars. The table is not intended to be exhaustive, but rather representative of the general nature of cultivar responses. Despite the great range of experimental growth conditions and UV doses utilized throughout these studies, large individual variation between cultivars was shown in response to UV-B radiation. Therefore, the potential for ameliorating the impacts of projected increases in solar UV radiation may be present in our current crop germplasm by selecting for UV tolerance. A pivotal concern must be acknowledged with this possibility, however: To date, we have little experimental evidence to indicate the mechanisms responsible for these cultivar differences. Since most crop cultivars are the descendants of a relatively small number of original genotypes, they are all rather closely genetically related. Differences in UV-B susceptibility then are not simply the result of gross morphological or structural differences such as those found between different plant species or growth forms such as grasses, herbs, shrubs and trees. Nor are they due to gross biochemical or physiological differences such as those known to occur between plants with different photosynthetic pathways (C<sub>3</sub>, C<sub>4</sub> or CAM). Therefore, these cultivar response differences must be due to more subtle character differences. Before crop breeding for UV

**Table 4. Relative Ranking of Cultivars Based Upon a Combined Growth Index. Plants Received a UV-B Dose Equivalent to a 16% Ozone Depletion (based upon generalized plant response function for College Park, Maryland, 39°N) during the summer solstice (data from Lydon et al. 1986)**

Cultivar	Greenhouse*	Field
Essex	-113	-75
Williams	-104	-41
Bay	-101	-37
James	-79	-27
York	+15	-6
Forrest	+253	+29

\* Relative ranking according to cultivar sensitivity was based upon the following:

$$\left( \frac{\text{dw UV-B} - \text{dw control}}{\text{dw control}} + \frac{\text{leaf area UV-B} - \text{leaf area control}}{\text{leaf area control}} + \frac{\text{ht UV-B} - \text{ht control}}{\text{ht control}} \right) \times 100$$

(dw = dry weight, ht = height)

Table 5. A Summary of Studies Examining Cultivar Differences in UV-B Radiation Sensitivity

Crop	Number of Cultivars	Growth Condition <u>a</u> /	Conclusions <u>b</u> /	Basis of Comparison <u>c</u> /	Reference
Glycine max	19	G.C.	20% tolerant 60% intermediate 20% sensitive	d.w.	Biggs et al. 1981
	2	G.H.	Cultivar Altona more sensitive than Bragg	d.w.	Vu et al. 1978
	23	G.H.	8% tolerant 33% unaffected 59% sensitive	d.w.	Teramura and Murali 1986
	5	F	20% sensitive 80% unaffected	seed d.w.	
Phaseolus vulgaris	2	G.H.& G.C.	BBL 290 more sensitive than Astro	leaf resistance	Bennett (1981)
	3	G.H.	Maxidor sensitive Saxa, Favorit tolerant		Dumpert and Boscher (1982)
Brassica oleracea	2	G.H.& G.C.	no difference	p.s. & d.w.	Van et al. (1976)
	2	G.C.	(?)		Garrard et al. (1976)
Cucumis sativus	5	G.H.	20% tolerant 80% sensitive	d.w.	Murali and Teramura (1986a)
	2	G.H.	Poinsett extremely sensitive, Ashley slightly sensitive	d.w.	Krizek (1978)
Tritium aestivum	4	G.H.	no difference (?)	d.w.	Dumpert and Boscher (1982)
	7	G.C.	no difference	d.w.	Biggs and Kossuth (1978)
	2	F	no difference	d.w.	Biggs et al. (1984)
Zea mays	4	G.C.	25% extremely sensitive 75% sensitive	d.w.	Biggs and Kossuth (1978)
Oryza sativa	5	G.C.	60% tolerant 40% sensitive	d.w.	Biggs and Kossuth (1978)

Table 5. A Summary of Studies Examining Cultivar Differences in UV-B Radiation Sensitivity  
(continued)

Crop	Number of Cultivars	Growth Condition <u>a/</u>	Conclusions <u>b/</u>	Basis of Comparison <u>c/</u>	Reference
Hordeum vulgare	4	G.H.	25% tolerant 75% sensitive	d.w.	Dumpert and Boscher (1982)
	3	G.C.	no difference	d.w.	Biggs and Kossuth (1978)
Spinacia oleracea	2	G.H.	both sensitive	d.w.	Dumpert and Boscher (1982)
Gossypium hirsutum	2	G.H.	no difference	d.w.	Ambler et al. (1975)
Pennisetum glaucum	2	G.C.	no difference	d.w.	Biggs and Kossuth (1978)
Cucurbita pepo	3	G.C.	no difference	d.w.	Biggs and Kossuth (1978)

a/ G.H. = greenhouse; G.C. = growth chamber; F = field

b/ If data presented, sensitive means UV-B radiation reduced d.w. by at least 10% over control plants. Tolerant indicates that UV-B resulted in less than 10% reduction in growth. In some cases, tolerant plants were even stimulated by UV-B radiation.

c/ d.w. = total plant dry weight; p.s. = net photosynthesis.

tolerance can be attempted experimentally, we must understand the genetic bases for these response differences. Otherwise, if tolerance to UV-B radiation were linked (in a genetic sense) to a suite of less desirable, or totally undesirable, characteristics, then crop breeding may not ameliorate, and could possibly exacerbate, the impacts of UV-B enhancement. In conclusion, there appears to be promising evidence that tolerant genotypes already exist in our current crop germplasm, supporting the notion that breeding may limit the deleterious impacts of increased solar UV radiation. However, a large degree of uncertainty still remains in connection with its implementation due to the absence of any information concerning the genetic bases for these differences.

## **2.E. Uncertainties in our current knowledge of UV-B effects on terrestrial ecosystems and plant growth forms**

Table 6 is a survey showing the 10 major terrestrial plant ecosystems in the world and their relative importance in terms of net primary productivity (NPP) and area covered. The effectiveness of UV-B radiation on plant growth has been examined in plants representing only 4 of these 10 ecosystems, and collectively these only account for 27% of global NPP. In two of these terrestrial plant ecosystems, temperate forests and temperate grasslands, only very limited preliminary data are currently available. The vast majority of our knowledge of the biological effects of increasing solar UV radiation stems from research focused upon agricultural crops, which account for less than 8% of global NPP.

A survey of UV-B studies by major plant growth forms is presented in Table 7. Of the 25 categories listed, in only 8 (32%) has the effectiveness of UV-B radiation on some component of plant growth (dry weight, photosynthesis, leaf area, height, etc.) been examined. Only very limited data exist for large, woody perennial plants (trees). There are virtually no data on the effects of UV-B radiation on lianas or vines, small woody shrubs, epiphytes, or lower vascular plants (ferns, lichens, mosses, and liverworts). Some data on the effects of UV-C (254 nm) radiation on lower vascular plants do exist, but since plant responses to UV-C radiation differ quantitatively as well as qualitatively from UV-B effects (Nachtwey 1975), these studies have been omitted from this analysis.

Of the 314 plant families in the world (Cronquist 1981), the effects of UV-B radiation have been examined in relatively few (Table 8). In approximately half these plant families where some knowledge of UV effects are known, the effectiveness of UV-B radiation on plant growth and development was not addressed. Instead, these studies focused upon epidermal transmission to UV or pollen germination. Therefore, in terms of utility for calculating the potential impacts of increasing levels of solar UV radiation on global productivity, relevant growth information exists for only about 19 families (6% of total). Of these 19 families, only 7 include representative species in which harvestable yield was examined (see Section 3.A, Direct Effects on Total Yield).

In conclusion, very little information exists on the effectiveness of UV-B radiation on native plant species. In fact, only a very small fraction of plant families and plant growth forms have actually been extensively examined



**Table 6. Survey of UV Studies by Major Terrestrial Plant Ecosystems (after Whittaker 1975)**

Ecosystem	Global NPP <sup>a/</sup> (10 <sup>9</sup> ton/yr)	Total Area (10 <sup>6</sup> km <sup>2</sup> )	Included in UV Study <u>b/</u>
Tropical forest	49.4	24.5	no
Temperate forest	14.9	12.0	yes
Savanna	13.5	15.0	no
Boreal forest	9.6	12.0	no
Agricultural area	9.1	14.0	yes
Woodland and shrubland	6.0	8.5	no
Temperate grassland	5.4	9.0	yes
Swamp and marsh	4.0	2.0	no
Desert and semidesert	1.7	42.0	no
Tundra and alpine areas	1.1	8.0	yes

a/ NPP = net primary productivity.

b/ Only studies examining some aspect of growth.

Table 7. Survey of UV Studies by Major Plant Growth Forms

Plant Growth Form	Included in UV Study *	Family
Large (>3 m tall) perennial plants		
Needle-leaved trees	yes	Pinaceae
Broad-leaved evergreen trees	yes	Rutaceae
Evergreen-sclerophyll trees	no	
Broad-leaved deciduous trees	yes	Aceraceae, Betulaceae Oleaceae
Thorn-trees	no	
Rosette trees	no	
Bamboos	no	
Lianas or vines	no	
Small (<3 m tall) perennial plants		
Needle-leaved shrub	no	
Broad-leaved evergreen shrub	no	
Evergreen-sclerophyll shrub	yes	Ericaceae
Broad-leaved deciduous	no	
Thorn-shrubs	no	
Rosette shrubs	no	
Stem succulents	no	
Suffrutescent shrubs	no	
Dwarf shrub	no	
Epiphytes	no	

Table 7. Survey of UV Studies by Major Plant Growth Forms  
(continued)

Plant Growth Form	Included in UV Study*	Family
Herbaceous plants		
Ferns	yes	Lemnaceae
Gramminoids	yes	Poaceae
Rosette plants	Yes	Polygonaceae
		Plantaginaceae
Forbs	yes	Amaranthaceae
		Asteraceae
		Chenopodiaceae
		Cruciferae
		Cucurbitaceae
		Euphorbiaceae
		Fabaceae
		Liliaceae
		Malvaceae
		Onagraceae
		Polygonaceae
		Rosaceae
		Scrophulariaceae
		Solanaceae
		Umbelliferae
Thallophytes		
Lichens	no	
Mosses	no	
Liverworts	no	

\* Only studies examining UV effects on some aspect of growth.

Table 8. A Survey of UV Studies by Plant Family

Family	No Species Examined	Native or Crop Species <u>a/</u>	Type of Study <u>b/</u>
Aceraceae	1	N	C
Amaranthaceae	1	N	C
Asteraceae	13	C/N	G, C, F*
Betulaceae	1	N	C
Bignoniaceae	1	N	F
Boraginaceae	1	N	F
Cactaceae	1	N	F
Capparidaceae	2	N	P, F
Chenopodiaceae	3	C/N	G, F*
Commelinaceae	1	H	P
Cruciferae	9	C/N	G, C, F*
Cucurbitaceae	6	C	G, F*
Cyperaceae	1	N	G
Ericaceae	3	C, N	G, F
Euphorbiaceae	1	H	G
Fabaceae	14	C/N	G, F*
Geraniaceae	4	N	P, F
Hippocastanaceae	1	N	F
Hydrocharitaceae	1	N	G
Lemnaceae	1	N	G
Liliaceae	5	C/N	G, F
Linaceae	1	N	F
Malvaceae	3	C	G, F
Oleaceae	1	N	C
Onagraceae	1	N	G, F
Oxalidaceae	1	N	G
Papaveraceae	1	N	P
Pinaceae	8	N	G
Plantaginaceae	2	N	G, C
Poaceae	23	C/N	G, C, F*
Polygonaceae	7	C/N	G, C, F
Portulacaceae	1	N	F
Rosaceae	3	N	C, F
Rutaceae	1	C	G
Salicaceae	1	N	F
Saxifragaceae	1	N	F
Scrophulariaceae	2	N	C, P
Solanaceae	5	C	G*
Umbelliferae	5	C	G, F

a/ C = crop; H = horticultural; N = native.

b/ C = competition study; F = epidermal transmittance study; G = growth study; P = pollination.

\*Included yield studies.

even in a cursory fashion. To address the larger question of the potential impact of enhanced levels of UV-B radiation on global terrestrial plant communities and ecosystems, we must currently make the unlikely assumption that perennial woody trees and shrubs respond in a fashion analogous to the responses of herbaceous annual agricultural species. Furthermore, we are completely lacking any experimental data on the interaction among various ecosystem levels and components under UV enhancement. Clearly, much more data would be necessary before any realistic estimates of this nature could be made.

## **2.F. Uncertainties in the ability to extrapolate effects of UV-B radiation on plants to the ecosystem level**

Ecosystem composition and function is dependent upon the influence of various biotic and abiotic factors. Changes in these factors can lead to alterations in species composition and proportion depending on the extent of change, initial species diversity, and genetic variability in resistance to change. Various plants and microorganisms show large genetic variation in UV resistance. In microorganisms particularly, such resistance can evolve rapidly. In higher plants, however, it is not yet known whether such evolution can occur within the timeframe in which the changes in UV-B radiation are anticipated. Therefore, it is presently not possible to predict the future evolutionary response to increases in UV-B radiation because of insufficient information on the inter- and intra-specific differences to UV-B radiation.

However, it could be generalized that if changes in UV-B radiation are large (by more than 100%) and the rate of change is rapid (occurring over a period of decades rather than centuries), then there will occur a large number of extinctions and extensive changes in ecosystem composition function due to differential sensitivity and response rates. If, on the other hand, change is small and occurs more gradually, there may be considerable evolutionary accommodation (Antonovics 1975). There is evidence that the evolution of UV resistance has been influential in the early history of life, and that species have developed protective mechanisms when exposed to higher levels of UV-B radiation (see Section 2.B, Issues Concerning Natural Plant Adaptations to UV Radiation). This genetic variation in UV resistance indicates that plants have the potential to evolve UV resistance. However, we still have only very preliminary data on the consequences of subtle shifts in species interactions, such as changes in competitive ability, upon future community and ecosystem composition. For example, Caldwell (unpublished report, 1985) has reported changes in competitive interactions between wheat and wild oats that may be associated with increased UV levels. Without a more complete understanding of such changes, further assessment on this area is currently not possible.

## **2.G. Uncertainties with the ability to extrapolate knowledge to higher ambient CO<sub>2</sub> environment**

Global atmospheric carbon dioxide (CO<sub>2</sub>) concentration has been gradually increasing over the centuries. Measurements of CO<sub>2</sub> concentration in ice cores from Greenland and Antarctica indicate an ambient CO<sub>2</sub> concentration of about 205 ppm some 20,000 years ago and approximately 280 ppm during the past 10,000 years (Neftel et al. 1982); values from 1905 indicate an early industrial level of about 290 ppm (Keelings 1978). Since 1957, both at Mauna Loa, Hawaii, and in Antarctica, atmospheric CO<sub>2</sub> concentration has been continuously monitored. The

records at Mauna Loa indicate that in 1968 the atmospheric CO<sub>2</sub> concentration was 317 ppm; today it is 340 ppm. In the decade between 1958 and 1969, the ambient CO<sub>2</sub> concentration increased by 0.7 ppm per year, while from 1970 to 1982 it increased by 1.3 ppm per year. It is anticipated that sometime between 2075 and 2100, the atmospheric CO<sub>2</sub> concentration will reach 600 ppm (Gates 1983). The major source contributing to the increase in CO<sub>2</sub> concentration has been the burning of fossil fuels. It is estimated that the world's remaining recoverable resources of oil, gas, and coal contain some  $4.13 \times 10^{12}$  metric tons of carbon. If this amount is burned and half remains airborne, the atmospheric CO<sub>2</sub> concentration would increase by a factor of four (Gates 1983).

At present we have no experimental evidence on the effects of enhanced levels of UV-B radiation under increased levels of atmospheric CO<sub>2</sub>. However, on the basis of other plant responses reported in the literature, some speculations could be made. It should be emphasized that these represent only potential, and not actual, circumstances. The individual effects of enhanced levels of UV-B radiation and increased atmospheric CO<sub>2</sub> concentration on various plant parameters are summarized in Table 9. In general, UV-B radiation has deleterious effects, while increased CO<sub>2</sub> has potentially beneficial effects on plant growth and development.

Photosynthesis is ordinarily inhibited by UV-B radiation but is increased by higher levels of CO<sub>2</sub> concentration, especially in C<sub>3</sub> plants. This results in a reduction of plant productivity by UV-B radiation and an increase in productivity by increased CO<sub>2</sub> concentration. Since CO<sub>2</sub> increases plant growth to a greater extent, the net effect of an interaction between UV-B radiation and increased levels of CO<sub>2</sub> may be a general compensation of the deleterious effects of UV-B radiation on plant productivity.

Water-use efficiency increases with an increase in CO<sub>2</sub> concentration due to decreased stomatal conductance and increased photosynthesis. On the other hand, in UV-B irradiated plants, water-use efficiency decreases due to the inhibition of photosynthesis. This results in increased drought tolerance with elevated ambient CO<sub>2</sub> concentration, and a decrease in tolerance with enhanced UV-B radiation. The net effect resulting between these two environmental changes would be a compensation of the increased drought tolerance by UV-B radiation.

Increased atmospheric CO<sub>2</sub> concentration has been shown to result in early flowering and accelerated maturity without a concomitant reduction in plant productivity. UV-B radiation inhibits flowering in some plants but stimulates flowering in others, with no apparent effect on maturity. The net anticipated effect of a combination of increasing levels of UV-B radiation and CO<sub>2</sub> concentration would be an increase in plant flowering and maturity which could then lead to longer-term changes in the pattern of community succession.

Responses to both increased levels of UV-B radiation and CO<sub>2</sub> concentration produce inter- and intraspecific variations, which could result in changes in the competitive balance among various plant associations (Gold and Caldwell 1983; Strain and Bazzaz 1983). The product of these two environmental changes could lead to an eventual alteration in plant composition and community structure. Changes in competitive balance could especially have adverse effects in agricultural systems if weeds increase their competitive advantage over crop plants. Since an increased need for weed control requires more tillage and/or

**Table 9. Summary of UV-B and CO<sub>2</sub> Effects on Plants (Lemon 1983; Teramura 1983).**

<u>Plant Characteristic</u>	<u>Enhanced UV-B</u>	<u>Doubling of CO<sub>2</sub></u>
Photosynthesis	Decreases in many C <sub>3</sub> and C <sub>4</sub> plants	In C <sub>3</sub> plants, increases up to 100% but in C <sub>4</sub> plants only a small increase
Leaf conductance	No effect in many plants	Decreases both in C <sub>3</sub> and C <sub>4</sub> plants
Water use efficiency	Decreases in most plants	Increases in both C <sub>3</sub> and C <sub>4</sub> plants
Dry matter production and yield	Decreases in many plants	In C <sub>3</sub> plants, almost doubles but in C <sub>4</sub> plants, only a small increase
Leaf area	Decreases in many plants	Increases more in C <sub>3</sub> than in C <sub>4</sub> plants
Specific leaf weight	Increases in many plants	Increases
Crop maturity	No effect	Accelerated
Flowering	May inhibit or stimulate flowering in some plants	Flowers produced earlier
Interspecific differences	Species may vary in degree of response	Major differences occur between C <sub>3</sub> and C <sub>4</sub> plants
Intraspecific differences	Response varies among cultivars	Response may vary among cultivars
Drought stress	Plants become less sensitive to UV-B but not tolerant to drought	Plants become more drought tolerant

herbicide application, the increase in production cost could render some crops uneconomical to produce, and thus potentially alter the economic importance of some plants.

It is predicted that an increase in CO<sub>2</sub> concentration would result in major climatic changes. Some regions of the world, including large portions of the central U.S. and much of eastern Europe and USSR, would experience serious decreases in precipitation, while the climates of Canada, Alaska, Western Europe, North and East Africa, and others may become wetter. Therefore, the great grain belts are predicted to become much drier (Gates 1983) and probably less productive. It has been shown that water stress increases plant tolerance to UV-B radiation (Teramura et al. 1984, Murali and Teramura 1986c). Thus, in these drier regions, UV-B radiation may not be as effective in reducing plant growth. Moreover, in the wetter regions, UV-B radiation may also not appreciably affect growth since increased levels of CO<sub>2</sub> would have the predominate effect.

The long-term effects of increased levels of atmospheric CO<sub>2</sub> are not fully known. However, it is projected that plant carbon:nitrogen (C/N) ratios would increase, and that the increase in the rate of plant succession would produce more organic matter available for decomposition. With high C/N ratios, the rate of mineralization would decrease due to limitations in the rate of decomposition, and thus the availability of nitrogen, phosphorus, and other nutrients might ultimately limit growth. Under mineral deficiency, plants have been demonstrated to be more tolerant to UV-B radiation (Murali and Teramura 1984a, 1984b). Although the relative impact of UV-B may be somewhat lessened by mineral deficiency, plant productivity and yield would nonetheless be deleteriously affected.

There is a very high degree of uncertainty in the assessment of these combined scenarios because of the lack of actual experimental data on the complex interactions between increased CO<sub>2</sub> concentration and UV-B radiation. In general, it appears that direct, negative effects of UV-B radiation on plant growth and development may be somewhat compensated by increased atmospheric CO<sub>2</sub> levels. However, the complex indirect effects resulting from changes in the competitive balance among species and changes in the quality and quantity of energy inputs into various ecosystem trophic levels cannot be assessed at this time. In light of the extreme importance of these interactions, the potential risks warrant great concern.

## **2.H. Uncertainties in the ability to extrapolate knowledge to include other atmospheric pollutants**

One of the growing environmental problems that has been of great concern to many industrialized countries is the increasing extent and occurrence of lower atmospheric air pollution. Primarily anthropogenic in origin, the major pollutants include ozone, sulfur oxides (SO<sub>x</sub>), and nitrogen oxides (NO<sub>x</sub>). All three major pollutants are deleterious to plant growth and development. According to the National Crop Loss Assessment Network, farm crop losses in the United States in 1981 due to air pollution amounted to between \$1 billion and \$2 billion. Ozone alone, or in combination with SO<sub>x</sub> and NO<sub>x</sub>, is responsible for up to 90% of the crop losses in the U.S. caused by gaseous air pollutants (Heck et al. 1982). The major sources of air pollutants are transportation vehicles,



industrial production facilities, and electrical power generation, each accounting for 60%, 16%, and 14% of the total, respectively (Mudd and Kozlowski 1975). The mechanism of ozone damage is through the destruction of the structural integrity of membranes, which impairs both membrane transport and ion uptake (Heath 1975). Sulfur dioxide affects photosynthesis through the lowering of pH, which results in chlorophyll destruction by loss of magnesium ions (Mudd 1975). The mode or target of injury of nitrogen dioxide ( $\text{NO}_2$ ) has not been fully examined. Some studies report that it may arise due to enzyme inactivation through acidification of the cell milieu (Tylor et al. 1975). Many investigators have studied plant responses to combinations of  $\text{O}_3$ ,  $\text{SO}_2$ , and  $\text{NO}_x$ . In most plants, the deleterious effects were additive and, in a few cases, multiplicative (Reinert et al. 1975).

UV-B radiation has been shown to inhibit photosynthesis through the inactivation of the reaction centers of PS II (Iwanzik and Tevini 1982, Tevini and Iwanzik 1983, Iwanzik et al. 1983), consequently reducing plant growth (Teramura 1983). At present, no data are available on the interaction between UV-B radiation and various air pollutants. However, since both UV-B radiation and various air pollutants independently have deleterious effects, their net interactions are anticipated to be additive or multiplicative. Because of the complete absence of experimental data, there is a high degree of uncertainty in this projection.

### 3. RISKS TO CROP YIELD RESULTING FROM AN INCREASE IN SOLAR UV-B RADIATION

#### 3.A. Direct effects on total yield

During the past 10 years, there have been nine field studies examining the effects of UV-B radiation on crop yield. Three other field studies have been reported (Caldwell et al. 1975, Caldwell 1983, Dumpert 1983); however, harvestable yield was not the focus of these studies. Combined, these nine studies included 22 crop species. The most widely examined species was corn (*Zea mays*), which was included in six of the nine studies, soybean (*Glycine max* found in four, and tomato (*Lycopersicon esculentum*), bean (*Phaseolus vulgaris*), and potato (*Solanum tuberosum*) each found in three studies. The relevant details of each study are listed in Table 10 and a brief summary follows below. A more comprehensive review of crop responses to UV-B radiation can be found in Appendix C (Effects of UV-B Radiation on the Growth and Yield of Crop Plants).

Ambler et al. (1978) grew eight species of crops (Table 11) in a field at Beltsville, Maryland (39°N). Species were paired and grown in six plots with a lamp irradiation system maintained 1.6 m above the plants. The irradiation system consisted of a linear arrangement of unfiltered Westinghouse BZS-CLG and FS-40 sunlamps. A two-dimensional gradient was established: one parallel to the lamps and another at right angles. Of the eight species examined, only one, broccoli, showed a significant UV effect (Table 10) although the authors suggested that sorghum and corn also were affected. There are two major areas of concern with the study. First, since unfiltered lamps emit both UV-B and UV-C radiation, both quantitative and qualitative effects must be reviewed with utmost caution (Nachtwey 1975). Second, where effects were reported, only significant differences were found for plants directly beneath the lamps, and not at a location farther away from lamps with the same (or higher) UV dose.

Table 10. Summary of Field Studies Examining the Effects of UV-B Radiation on Crop Yields.  
 Values represent percent changes from controls

	Ambler et al. (1978) (1)	Bartholic et al. (1975) (2)	Becwar et al. (1982) (3)	Biggs and Kossuth (1978) (4)	Biggs et al. (1984) (4)	Eisenstark et al. (1984) (4)	Esser (1980) (5)	Hart et al. (1975) (1)	Teramura (1981)(1982)(1983) (4)		
Cucurbita maxima	0										
Cucurbita pepo				-14 to -90							
Phaseolus vulgaris	0	+12 to +15					+53 to -75				
Triticum aestivum					-5						
Zea mays	0	+29 to +39		0	0	-79 to -87		0			
Spinacia oleracea							+11 to -56				
Sorghum bicolor	0										
Capsicum annum								-(?)			
Glycine max	0				0			0	-8	0	0
Cynodon dactylon											
Beta vulgaris	0										
Brassica oleracea var. capitata							+19 to -49				
Brassica oleracea var. botrytis	-24 to -45%										
Lycopersicon esculentum		-5 to -26		-11 to -39				0			
Nicotiana tobaccum								0			
Raphanus sativus			0								
Pennisetum glaucum								0			
Solanum tuberosum			0	0			-2 to -41				
Brassica juncea				-9 to -43							
Vigna unguiculata				-18 to -38							
Oryza sativa					0						
Arachis hypogaea				0				0			

(1) Unfiltered Westinghouse BZS-CLG and FS-40 sunlamps

(2) Ambient UV filtered with Mylar Tape S or polyethylene

(3) Ambient UV filtered with cellulose acetate, Aclar, or Mylar

(4) Westinghouse FS-40 sunlamps filtered with cellulose acetate or Mylar

(5) Unfiltered Philips TL 40/12 sunlamps and lamps filtered with Schott WG 305 (2 and 3 mm) filters

Table 11. Details of Field Study by Ambler et al. (1978) a/

Crop	Yield Character <u>b/</u>	Percent Change	Significance <u>c/</u>
Cucurbita maxima (squash)	fruit f.w.	-23 to -26	ns
Phaseolus vulgaris (bean)	fruit f.w.	+2 to -12	ns
Glycine max (soybean)	seed d.w.	+0.3 to 3	ns
Beta vulgaris (sugar beet)	root f.w.	-34 to -46	ns
Sorghum bicolor (sorghum)	shoot f.w.	-14 to -15	ns (P=0.3)
Zea mays (corn)	ear f.w.	-24 to -44	ns (P=0.2)
Brassica oleracea var. botrytis (broccoli)	fruit f.w.	-24 to -45	(P=0.01)

a/ Irradiation system used was unfiltered Westinghouse BZS-CLG and FS-40 sunlamps; the percent ozone change cannot be calculated due to the inclusion of UV-C radiation.

b/ f.w. = fresh weight, d.w. = dry weight

c/ ns = not significant

Therefore, shading may be a complicating factor in this study, although this possibility was not discussed.

Bartholic et al. (1975) conducted field exclusion studies in Gainesville, Florida (29° 36'N) where ambient levels of UV-B were filtered through plastic films of Mylar Type S or polyethylene (Table 12). Since plants were grown under panels covered with these films, only the direct beam component of ambient UV was removed (which represents approximately one-half the total ambient UV present). Three crop species were tested (beans, corn, and tomato), and each treatment was replicated five times in three m<sup>2</sup> plots. Compared with uncovered plots, total bean yields under Mylar decreased 15% and under polyethylene by 11%. In corn, Mylar reduced yield by 28% and polyethylene by 23% compared with uncovered plots, resulting in a 30-40% increase in ear fresh weight in plants growing under ambient levels of UV-B. Tomato matured significantly earlier under Mylar, resulting in an apparent decrease in fruit weight in plants growing in uncovered plots. Although no data were given, these authors did mention the possibility of confounding spidermite damage in the corn study. Apparently, there was a significant effect of growing plants under the plastic panels compared with uncovered plants. Despite both materials being reported as reducing PAR (photosynthetically active radiation) by only 7% each, there may have been a shading problem associated with the panel framework. Alternatively, a difference may have been maintained in leaf temperatures or soil moisture as a direct result of the enclosures themselves.

The study by Becwar et al. (1982) was also an exclusion study (Table 13) located at 3000 m in the Colorado Rocky Mountains (39° 11'N). Three types of filters were used: Mylar, Aclar, and cellulose acetate. Four crop species were examined including Alaska pea (*Pisum sativus*), potato, radish (*Raphanus sativus*), and wheat (*Triticum aestivum*). Plants were grown in pots with peat, vermiculite and sand. The only UV effect reported was a decrease in wheat height (between 8% and 19%, depending upon plant age), with no corresponding change in total plant dry weight. A second study was also conducted at the high elevation field site using filtered FS-40 sunlamps, which supplemented ambient levels of solar UV-B. Lamps were held in standard two-lamp fluorescent fixtures and filtered with cellulose acetate and Mylar. These were suspended 1.1 m above the plants and produced no significant effect on crop yield despite a calculated 52% UV enhancement (based on the generalized plant action spectrum by Caldwell, 1971) compared with sea level irradiances at the same latitude. Unfortunately, there were no plants grown under a UV irradiance that simulated the dose plants received at sea level as control to make actual comparisons.

Biggs and Kossuth (1978) grew nine crops (Table 14) in raised beds filled with a synthetic soil mix in Gainesville, Florida (29° 36'). Yield data were reported for seven of the nine crops. UV-B radiation was supplemented in the field with a linear arrangement of six FS-40 sunlamps mounted end-to-end and kept at a 12° angle relative to the soil surface. This produced a "gradient" in UV-B irradiances. Control plants were those growing without lamps above them adjacent to those receiving the highest UV dose. Although "significant" UV effects were reported in half the plants, no indication of the statistical tests used were found in the report, nor were other descriptive statistics given (such as S.D. or S.E.). One area of concern was the lack of consistency of effects in this study. For instance, the greatest reductions in yield were

Table 12. Details of Field Study Excluding Ambient Solar UV  
by Bartholic et al. (1975) a/

Crop	Yield Character <u>b/</u>	Percent Change	Significance
Zea mays (corn)	ear f.w.(?)	+29 to +39	P=0.05
Lycopersicon esculentum (tomato)	fruit f.w.(?)	-5 to -26	(?)
Phaseolus vulgaris (bean)	fruit f.w.(?)	+12 to +15	P=0.05

a/ Irradiation system used was Mylar and polyethylene exclusion panels of ambient UV; ozone was simulated to increase

b/ f.w. = fresh weight

Table 13. Details of Field Study Excluding Ambient Solar UV  
by Becwar et al. (1982) a/

Crop	Yield Character <u>b/</u>	Percent Change	Significance <u>c/</u>
Raphanus sativus (radish)	root d.w.	+11 to +20	ns
Solanum tuberosum (potato)	tuber d.w.	-1 to -17%	ns

a/ Irradiation system used was Mylar, Aclar, and cellulose acetate exclusion panels for ambient UV and filtered FS-40 sunlamps; ozone was simulated to increase

b/ d.w. = dry weight

c/ ns = not significant

Table 14. Details of Field Study by Biggs and Kossuth (1978) a/

Crop	Yield Character <u>b/</u>	Percent Change	Significance <u>c/</u>
Solanum tuberosum <u>c/</u> (potato)	tuber f.w.(?)	+2 to -21	ns
Lycopersicon esculentum (tomato)	fruit f.w.(?)	-11 to -39	P=0.05(?)
Zea mays (corn)	ear dia.	-3 to +1	ns
Vigna unquiculata (blackeye pea)	fruit f.w.(?)	-18 to -38	P=0.05(?)
Arachis hypogaea (peanut)	fruit d.w.(?)	0 to -24%	ns
Cucurbita pepo (squash)	fruit f.w.(?)	-14 to -90	P=0.05(?)
Brassica juncea (mustard)	leaf f.w.	-9 to -43	P=0.05(?)

a/ A gradient of UV-B irradiances was produced by using a linear arrangement of sunlamps (cellulose acetate filtered FS-40). Plants without lamps above them were controls receiving no supplement UV-B irradiation.

b/ f.w. = fresh weight

c/ ns = not significant

often found in plants growing in the lowest UV irradiance, or the largest UV effects were found in plants growing adjacent to ones showing little or no effect. By using a gradient, essentially each plant received a uniquely different UV dose, therefore plants and treatments must, by necessity, be pooled for statistical analysis. Such data manipulation would almost certainly add a great deal of experimental variability and lead to further difficulty in interpretation.

In another field experiment, Biggs et al. (1984) studied the effects of UV radiation on crop yield over the course of several growing seasons in four field-grown species including rice (*Oryza sativa*), wheat, corn, and soybean (Table 15). Again, plants were grown in raised beds filled with synthetic soils, but in this instance UV irradiation was not supplied as a gradient. Instead, each system contained six FS-40 sunlamps (three rows of two linearly arranged lamps) filtered with 3-, 5-, or 10-ml cellulose acetate providing 32%, 23%, or 16% UV enhancements (based on the generalized plant action spectrum) above ambient. Control plants were grown under Mylar-filtered lamps. Despite relatively large reductions in rice yield (up to 50%), these were not found to be statistically significant. The only significant yield reduction reported was for wheat (5% reduction) and only for one of the two experimental years. The data for rice, corn, and soybean were highly variable and therefore only very substantial changes could be statistically detected. The underlying reasons for this high degree of variability are presently unknown.

Eisenstark et al. (1984) grew corn (Table 16) for three growing seasons in Columbia, Missouri (38° 57'N). Plants were grown in large pots and irrigated during the study. Two levels of UV radiation were supplied by cellulose-acetate-filtered FS-40 sunlamps simulating a 7% and 21% ozone depletion (based upon the generalized plant action spectrum). There were two types of controls: in one, plants were grown under lamps filtered with Mylar, and in the second, plants were grown without overhead lamps. In the most recent field study, half the plants were irradiated 4 weeks after germination (vegetative) and the other half, at tassel formation (reproductive). Plants were found to be particularly susceptible to UV-induced effects during tassel development (Eisenstark and Perrot 1985). In plants irradiated as seedlings, 7% and 21% ozone reductions produced total grain yield reductions of 23% and 32%, respectively, when compared with Mylar control plants.

However, even larger differences were found when plants grown under either Mylar or cellulose-acetate-filtered lamps were compared with those grown without overhead lamps. In this case, yield was reduced by 80% in plants filtered by Mylar and 87% in those grown under cellulose acetate. Even more dramatic was the differential ear maturation: 59% matured when grown in sunlight without overhead lamps, none matured under cellulose-acetate-filtered lamps and only 18% matured under Mylar-filtered lamps. Although the authors suggest that this large lamp effect is perhaps due to the additional UV-A emitted from the sunlamps, this UV-A supplement is very small (only several percent) relative to that UV-A present in midday solar radiation (see Caldwell et al. 1984). At present, these responses are not well understood and certainly need to be clarified.

Esser (1980) conducted field studies in Frankfurt, Federal Republic of Germany (50° N), on six crop species, but yield was only reported in four:



Table 15. Details of Field Study by Biggs et al. (1984) and Biggs (1985) a/

Crop	Yield Character <u>b/</u>	Percent Change	Significance <u>c/</u>
Oryza sativa (rice)	seed d.w.	-26 to -47	ns
	no. seed heads	-18 to -50	ns
Triticum aestivum (wheat)	seed d.w. (1982)	-5	P=0.05(?)
	seed d.w. (1984)	0	ns
Zea mays (corn)	ear f.w.	(?)	ns
Glycine max (soybean)	pod d.w.	(?)	ns

a/ Irradiation system used was cellulose acetate and Mylar-filtered FS-40 sunlamps; ozone was simulated to decrease by 16%, 23%, and 32%.

b/ d.w. = dry weight; f.w. = fresh weight

c/ ns = not significant

Table 16. Details of Field Study by Eisenstark et al. (1985)

Crop	Yield Character	Percent Change	Significance	Simulated Ozone Change (%)	Irradiation System
Zea mays (corn)	grain dry weight	-87	P=0.05	-7, -21	Cellulose acetate- and Mylar-filtered FS-40 sunlamps

bean, cabbage (*Brassica oleraceae* var. *capitata*), spinach (*Spinacia oleracea*) and potato (Table 17). He used linearly arranged Philips TL 40/12 sunlamps suspended 3 m above the plants and produced four UV enhancements using a combination of reflectors and Schott WG305 filters. His two highest UV doses, simulating 40% and 15% ozone reductions (based on the generalized plant action spectrum) were produced by using unfiltered lamps. Although significant yield reductions were found in the four crops tested, these were only found under unfiltered lamps. In fact, yields for spinach, cabbage, and bean appeared to increase under filtered lamps.

Hart et al. (1975) grew plants (Table 18) under unfiltered FS-40 sunlamps at Beltsville, Maryland (39° N). Lamps were linearly arranged and suspended 3.7 m above the ground. Almost no other details of the experiment were given and no actual yield data are presented. Only a short descriptive summary of the results are reported in a table. Because of the complete absence of data, this study may only be useful in a very qualitative way. Even in this light, one must be careful with any interpretations drawn from this study due to the presence of UV-C radiation from these unfiltered lamps.

Teramura has grown soybeans for five seasons (Table 19) at a farm owned and operated by U.S.D.A. in Beltsville, Maryland (39° N). During the first two years, six different soybean cultivars were grown under filtered FS-40 sunlamps oriented perpendicular to the soybean rows (rows oriented in an east-west direction). This arrangement avoids the large variation in UV irradiance along the length of the bulb, which is a major problem with linearly arranged (end-to-end) lamps. (See Section 5, Recommendations.) Control plants were grown under Mylar-filtered lamps. In the last three years, only two cultivars were grown to increase the sample size to at least 200 plants per cultivar per treatment. Field experiments simulated 0, 5%, and 16% ozone depletions (based on the generalized plant action spectrum) during the first year and 0, 16%, and 25% ozone depletions thereafter. Significant reductions in crop yield were found only in 1981 for cultivars Essex and James. Interestingly, total seed yield/plant was significantly increased in cultivar Williams during this same year. Although similar general trends were found in 1982, there were no significant differences associated with increasing UV-B radiation. Yield was decreased in cultivar Essex and increased in cultivar Williams, in 1984, 1985, and 1986, by supplemental UV-B. In 1983, a substantially higher yield per plant (on a relative basis) was found in cultivar Essex, which was opposite to that observed in the previous 2 years. One critical caveat that must be included with this observation is that 1983 was an extremely dry year. Actual seed weights of control plants during 1983 were only 20-30% of those harvested in 1981 and 1982. Therefore, it is rather tentative whether these 1983 data are representative of true (normal) field trends. This graphically illustrates the importance of multiyear studies to obtain a more representative description of the potential impacts of an increase in solar UV radiation reaching the surface of the earth. It also emphasizes the need to monitor other environmental variables in addition to UV radiation.

Soybean yield is influenced by microclimatic factors as well as total UV-B dose. Yield appears to be strongly influenced by the number of days of precipitation, the number of days when maximum temperature exceeds 35°C, and the number of days where total irradiance is low (i.e., cloudy days).

Table 17. Details of Field Study by Esser (1980) a/

Crop	Yield Character <u>b/</u>	Percent Change	Significance
Solanum tuberosum (potato)	tuber f.w.	-2 to -41	P=0.05(?)
Spinacia oleracea (spinach)	leaf f.w.(?)	+11 to -56	P=0.05(?)
Brassica oleracea var. capitata (cabbage)	leaf f.w.	+19 to -49	P=0.05(?)
Phaseolus vulgaris (bean)	fruit f.w.(?)	+53 to -75	P=0.05(?)

a/ Irradiation system used consisted of unfiltered Philips TL 40/12 and Schott WG305 filtered TL 40/12 sunlamps; ozone was simulated to decrease by 3%, 8%, 15%, and 40%.

b/ f.w. = fresh weight

Table 18. Details of Field Study by Hart et al. (1975) a/

Crop	Yield Character <u>b/</u>	Percent Change	Significance <u>c/</u>
Lycopersicon esculentum (tomato)	fruit no. fruit size	no data given no data given	ns ns
Capsicum annuum (bell pepper)	fruit size fruit no.	no data given	ns P=0.05(?)
Zea mays (corn)	grain wt.	no data given	ns
Glycine max (soybean)	bean wt.	no data given	ns
Arachis hypogaea (peanut)	nut wt.	no data given	ns
Pennisetum glaucum (pearl millet)	shoot d.w.(?)	no data given	ns
Cynodon dactylon (Bermuda grass)	shoot d.w.(?)	no data given	ns

a/ Irradiation system used consisted of unfiltered FS-40 sunlamps; ozone change cannot be calculated due to the inclusion of UV-C radiation.

b/ d.w. = dry weight

c/ ns = not significant

Table 19. Details of Field Study by Teramura (1981-1985) that Measured Percent Change in Seed Dry Weight of Soybean (*Glycine max*) from a Simulated Decrease in Ozone<sup>a</sup>

Cultivar	Simulated Ozone Change (%)										
	1981		1982		1983		1984		1985		1986
	-16	-16	-25	-16	-25	-16	-25	-16	-25	-16	-25
Bay	-10	+6	-8								
Essex	-25 <sup>b</sup>	-12	-23	+39 <sup>b</sup>	+6	+14 <sup>b</sup>	-7	+6	-20 <sup>b</sup>	-5	-19 <sup>b</sup>
James	-14 <sup>b</sup>	-22	-25								
Williams	+22 <sup>b</sup>	+9	+14	+13 <sup>b</sup>	-11 <sup>b</sup>	+15 <sup>b</sup>	+10 <sup>b</sup>	+18 <sup>b</sup>	+4	+8	+6
York	-12	-25 <sup>b</sup>	-8								
Forrest	--	-14	+27								

<sup>a</sup> Irradiance was provided by Mylar (control) and cellulose acetate (UV-B supplement) filtered FS-40 sunlamps.

<sup>b</sup> Significantly different from controls at P<0.05 level.

After initially screening 23 cultivars in the greenhouse, 6 were chosen for field experimentation. These six were picked because they represented the range of UV sensitivity found in the greenhouse, including very sensitive as well as very tolerant cultivars. Beginning in 1983, only Essex, a very sensitive, and Williams, a very tolerant cultivar were planted in the field to increase experimental sample sizes to 200 plants per treatment. As the table above shows, yields for Essex were generally reduced by the higher UV supplementation (25% ozone depletion) while the lower supplementation showed variable results. In the UV-tolerant cultivar Williams, a 16% ozone depletion generally increased yield, with much more variable results found at the higher ozone depletion. One important point to be made is that the sensitive cultivar Essex is currently replacing other older cultivars, including Williams, and is becoming one of the most widely planted soybeans in the U.S. This is because Essex has other features that crop breeders find superior to Williams. In a UV-enriched environment, however, Essex will be deleteriously affected. Therefore, superior cultivars that crop breeders are developing today may not be suitable for the future should the environment change.

Interestingly, the total amount of precipitation received is not nearly as important as is its distribution over the growing season. In general, yield decreases as the number of hot days increases, and increases as the number of days with precipitation approaches 25 in the growing season. Further increases in the number of days with precipitation decrease yield. Overall, those microclimatic factors that induce plant water stress (i.e., sunny, hot days with widely dispersed precipitation) reduce yield, while conditions of reduced water stress (i.e., cloudy, cooler days with frequent precipitation) enhance yield up to a threshold point when yield is again reduced. By contrast, the effects of UV-B appear to be more pronounced in years when microclimatic factors favor high yield. The effects of UV-B have been shown to be masked under conditions of plant water stress (Murali and Teramura 1986c). The relative importance of UV-B is a function of the cultivar and other prevailing microclimatic factors. For example, in Essex, total seed yield can be predicted within 95% confidence intervals with a regression model which includes total UV-B dose, number of precipitation events, and the number of days where air temperature exceeds 35°C as predictor variables.

Despite the broad range of experimental protocols and dosimetry used by various investigators, it appears that increases in solar UV radiation penetrating to the earth's surface could potentially have a deleterious impact upon global crop yields. Even discounting the data from the three unfiltered lamp studies (Ambler et al. 1978, Esser 1980, Hart et al. 1975), there are still more instances of significant reductions in yield than reports of no effect at all. The uncertainty associated with this conclusion is moderate to large, since all these studies were imperfect validations, suffering from one problem or another in experimental design or dosimetry. Furthermore, only three studies (Biggs et al. 1984, Eisenstark et al. 1984, and Teramura 1981-1984) include multiyear observations where longer-scale environmental variability has been taken into consideration. Even small reductions in yield can have enormous consequences when considering the fine balance of the economics of modern agriculture. Therefore the data concerning the effects of increasing UV radiation to global agricultural productivity imply large risks and warrant great concern.

### **3.B. Risks to yield due to a decrease in quality**

The quality of crop yield has only been quantitatively examined in a few limited studies. Biggs and Kossuth (1978) reported differences in the quality of tomato and potato yields from field trials conducted in Gainesville, Florida (see previous section on crop yield). In that study, they reported that the number of abnormally shaped tomato fruit (called defective in the study) decreased under enhanced levels of UV-B radiation supplied from filtered FS-40 sunlamps. The range of this reduction in defective fruit was from 11% to 41% compared with ambient grown controls; however, there was no clear relationship between the magnitude of this reduction and UV-B dose. They also reported a 6% to 23% reduction in the number of culls (rots, cracks, sunscald, etc.) in plants receiving moderate UV-B enhancements, while those receiving low enhancements of UV-B radiation produced a 10-34% increase in culls. Again, there was not a simple, linear relationship between UV dose and the number of culls produced.

Biggs and Kossuth (1978) also report a 3-13% increase in the mean potato weight of grade A large potatoes under enhanced levels of UV-B radiation, but

not in any other grade categories. Again, there did not appear to be a specific UV-B dose-response relationship for this observation. In both tomato and potato, no data were included to indicate whether these differences were significant, and if so, the specific statistical tests used to determine this.

In a field study conducted in Beltsville, Maryland, Ambler et al. (1978) examined the effects of UV radiation supplied from unfiltered sunlamps. They reported that the sugar content in sugar beet significantly increased between 17% and 21% with increasing UV-B irradiance. However, they only observed these significant increases in plants directly beneath the lamp irradiation system and not in plants receiving an identical UV-B dose at some distance away. This suggests that some other uncontrolled factor (shading?) was inadvertently introduced into the experiment. Additional experiments are needed to clarify this point.

A study conducted by Teramura (1982-1985) examined the effects of UV-B radiation on seed protein and lipid concentrations of soybean plants grown in the field at Beltsville, Maryland. A summary of those data are presented in Table 20 for the six cultivars tested in 1982 and the two cultivars tested in 1983 and 1984. Overall, the effects of UV radiation were relatively small. For example, seed protein concentrations did not change by more than 5%, and lipids not more than 13%, over all cultivars and treatments for both years. Nonetheless, significant UV effects were detected. Seed protein concentrations declined by as much as 5% during both the 1981 and 1982 growing seasons in cultivar Essex. Seed lipid concentrations were reduced by 3-5% in cultivar Forrest in 1982, the only year in which this character was measured in Forrest. Interestingly, lipid concentrations increased during both years in cultivar Williams, although this increase was only significant for the 1982 harvest. Williams is a cultivar whose seed quality and total seed yield (see Table 20) were positively affected by UV-B enhancements, while Essex is generally deleteriously affected.

In addition to direct losses in yield (reductions in quantity), increasing levels of UV-B radiation also may affect yield quality as shown above by several investigators. The extent of UV-mediated alterations in global yield quality cannot presently be estimated with any degree of confidence, due simply to the lack of experimental data for different species. Furthermore, conclusions drawn from a single growing season may be unreliable due to the interactions apparently involved between UV-B radiation and other commonly experienced plant stresses (see Section 2.C, Issues Associated with the Extrapolation of Data from Controlled Environments into the Field). Nonetheless, evidence collected over several years show consistent reductions in yield quality in soybean, suggesting that the risk to yield may be quite high in other crops as well.

### **3.C. Risks to yield due to possible increases in disease or pest attack**

Six studies that examined the effects of UV-B radiation on the severity of pests and diseases are summarized in Table 21. Esser (1980) reported that the number of aphids per bean plant was significantly decreased by UV-B radiation 11 days after their introduction, but there was no significant difference in the spidermite population 7 days after their application. Although the results suggest that UV-B radiation can have potentially beneficial effects on pest control, these conclusions must be judged with caution since the observation period was less than 2 weeks long. Whether there would be any longer-term



Table 20. Summary of Changes in Yield Quality in Soybean Between the 1982 and 1985 Growing Seasons  
(Teramura 1982-1985)

Crop	Yield Character	1982 % Change	Signi- ficance	1983 % Change	Signi- ficance	1984 % Change	Signi- ficance	1985 % Change	Signi- ficance	1986 % Change	Signi- ficance
Glycine max											
cv Bay	% protein	0 to -5	ns*								
	% lipid	-1.4 to +3	ns								
Essex	% protein	-3 to -5	P=0.05	+1 to -5	P=0.05	+1 to 0	ns	-0.7 to 0	ns	0 to -1	ns
	% lipid	-2 to +.5	ns	+2 to -2	ns	-2 to 0	ns	0	ns	0 to -2	P=0.05
James	% protein	+2 to +3	ns								
	% lipid	-1 to -2	ns								
Williams	% protein	0 to -.2	ns	+4 to -.2	ns	+3 to +5	P=0.05	-0.5 to -1	P=0.05	-1 to -3	P=0.05
	% lipid	+5 to +8	P=0.05	-1 to +6	ns	-5 to -10	P=0.05	0	ns	0 to +1	P=0.05
Forrest	% protein	+5 to +8	ns								
	% lipid	-3 to -5	P=0.05								
York	% protein	-2 to -3	ns								
	% lipid	0 to +3	ns								

\* ns = not significant

Table 21. Summary of UV-B Effects on Plant Pests and Diseases

Pest or Disease	Host Plant	UV-B Irradiance <u>a</u> /	Conclusion <u>b</u> /	Reference
Aphids ( <i>Aphis fabae</i> )	bean	6-25% $O_3$ depl.	decreased no. by 79-81%	Esser 1980
Spidermite ( <i>Tetranychus uticae</i> )	bean	6-25% $O_3$ depl.	-15 to +3% change (n.s.)	
Rust ( <i>Uromyces striatus</i> )	alfalfa	55-93 $mWm^{-2}$	-1 to -2% change in spore germination (n.s.)	Carns et al. 1978
Scab ( <i>Cladosporium cucumerinum</i> )	cucumber	55-93 $mWm^{-2}$	-4 to -11% change in spore germination (n.s.)	
		8-112 $mWm^{-2}$	disease severity unaffected	
Early blight ( <i>Alternaria solani</i> )	tomato	55-93 $mWm^{-2}$	-1 to 2% change in spore germination (n.s.)	
		8-112 $mWm^{-2}$	disease severity unaffected	
Leaf spot ( <i>Stemphylium botryosum</i> )	alfalfa	55-93 $mWm^{-2}$	-2 to 2% change in spore germination (n.s.)	
		8-112 $mWm^{-2}$	disease severity unaffected	
Anthracnose ( <i>Colletotrichum lagenarium</i> )	cucumber	55-93 $mWm^{-2}$	spore germination decreased 33 to 89%	
		8-112 in $Wm^{-2}$	disease severity decreased with UV-B by 33-66%	
Black rot ( <i>Mycosphaella melonis</i> )	cucumber	55-93 $mWm^{-2}$	spore germination decreased 10-60%	
		8-112 $mWm^{-2}$	disease severity decreased	
Scab ( <i>Cladosporium cucumerinum</i> )	cucumber	80-800 $Wm^{-2}$ (unweighted)	spore germination decreased by 10-40%	Owens and Krizek 1980

Table 21. Summary of UV-B Effects on Plant Pests and Diseases (continued)

Pest or Disease	Host Plant	UV-B Irradiance <u>a/</u>	Conclusion <u>b/</u>	Reference
Rust ( <i>Uromyces phaseoli</i> )	bean	4.8-20 mWm <sup>-2</sup>	infected leaves decreased by 61%	Esser 1980
Rust ( <i>Puccinia coronata</i> )	oats	4.8-20 mWm <sup>-2</sup>	infected leaves decreased by 30-44%	
Powdery mildew ( <i>Erysiphe graminis</i> )	wheat	4.8-20 mWm <sup>-2</sup>	infected leaves decreased by 90-100%	
		10-20 mWm <sup>-2</sup>	99% reduction in conidia	Esser (1979)
Leaf rust ( <i>Puccinia recondita</i> )	wheat	8-16% O <sub>3</sub> depl.	infection decreased 14-67% (n.s.)	Biggs et al. 1984
Glume blotch ( <i>Septoria nodorum</i> )	wheat	8-16% O <sub>3</sub> depl.	infection decreased 12-14% (n.s.)	
Leaf spot ( <i>Helminthosporium sativum</i> )	wheat	8-16% O <sub>3</sub> depl.	infection decreased 4-6% (n.s.)	
Frog eye spot ( <i>Cercospora</i> sp)	soybean	8-16% O <sub>3</sub> depl.	0-10% change in seed infection (n.s.)	
Seed blight ( <i>Phomopsis</i> sp)	soybean	8-16% O <sub>3</sub> depl.	0-6% change in seed infection	
Leaf virus (Potato virus S)	Chenopodium quinoa	25-110 mWm <sup>-2</sup>	44% decrease in lesion no.	Semeniuk and Goth 1980

a/ Weighted with generalized plant action spectrum.

b/ n.s. = not significant

differences in pest attack is yet unknown. Field studies (Esser 1980) detailing crop growth under enhanced UV-B radiation do not report any difference in natural pest attack among UV-B treatments.

The severity of some crop diseases has also been studied under laboratory, greenhouse, and field conditions (Table 21). Studies by Carns et al. (1978) on in-vitro spore germination of six fungal pathogens showed that hyaline spores are more sensitive to UV-B radiation than are pigmented spores. Their tests conducted on plants grown in growth chambers also showed a similar relationship. Owens and Krizek (1980), however, found that in a pigmented spore (*Cladosporium cucumerinum*), survival was decreased with UV-B radiation. This was due more to a delay in germ tube emergence than complete inhibition of growth. Other studies (Esser 1980, Biggs et al. 1984) also indicate that there is not any clear relationship between spore coloration and UV-B radiation effectiveness.

Short-term growth chamber studies by Esser (1980) on three leaf fungal pathogens showed a significant decrease in disease severity with UV-B radiation (Table 21). In contrast, a field study by Biggs et al. (1984) showed no significant difference in disease severity on leaves or seeds under increased UV-B radiation. However, when leaf rust-resistant and rust-sensitive cultivars of wheat were tested, Biggs et al. (1984) and Biggs (1985) found that in the sensitive cultivar there were no differences up to 60 days after planting, while 119 days after planting, disease severity increased with UV-B radiation. In the resistant cultivar, there were no differences in disease severity. These results suggest that the effects of UV-B radiation on plant diseases can vary with pathogen, plant species, and cultivar.

Semeniuk and Goth (1980) found significant UV-B-mediated reductions in potato virus infection on *Chenopodium quinoa*. At irradiances over  $86 \text{ mW m}^{-2}$  UV-B<sub>BE</sub> (weighted with generalized plant action spectrum), no infection occurred. In this study, virus extract was exposed to UV-B radiation immediately upon its application over the leaf surface. Intuitively, viruses should be highly susceptible to UV-B radiation since they only contain nucleic acids covered with proteins, both of which have high UV absorption properties. Furthermore, viroids, which are devoid of a protein coat, may be more susceptible despite their small size. These effects would probably be greatest when the virus or viroids are directly exposed to UV-B radiation as may happen during mechanical transmission. Virus or viroids transmitted through seed, pollen, insects, mites, nematodes, and fungi may not be as susceptible to UV-B radiation, due to the additional cellular screening offered by the host tissues.

One of the plant defense mechanisms that inhibits fungal development is the production of a class of chemicals known as phytoalexins (Bell 1981). Uehara (1958) first demonstrated the existence of phytoalexins in soybeans, and later Klarman and Gerdemann (1963) demonstrated their importance in disease resistance. Phytoalexin production in plants can be induced artificially through mechanical injury, high temperature, the application of fungicides and antibiotics, and by UV-C radiation (Bridge and Klarman 1973, Reilly 1975). It is suggested that thymine dimers produced after UV-C absorption by DNA are involved in the synthesis of phytoalexins (Reilly 1975). UV-B radiation also induces isoflavonoid phytoalexin synthesis (Bakker et al. 1983), thereby possibly having an antifungal effect on plants; however, excess production can be toxic due to free radical formation (Beggs et al. 1984).

At present it is difficult to forecast the consequences of enhanced UV-B radiation in terms of pest and disease damage. From the limited information available, it appears that in some cases UV-B radiation might decrease disease severity, while in others it might aggravate it. Coupled with reduced vigor in plants sensitive to UV-B radiation, an increase in disease severity could pose a considerable risk, resulting in substantial losses in crop yield. Further studies are obviously needed to develop a better understanding of the consequences of increased levels of UV-B radiation on pests and plant diseases.

### 3.D. Risks to yield due to competition with other plants

The following is a summary of the potential impacts of the interactions between UV-B radiation and plant competition. A more comprehensive review can be found in Gold and Caldwell (1983). Plant resistance to a change in an environmental stress is, in part, a genotypically controlled, species-specific characteristic (Levitt 1980). An alteration of an environmental stress could thus lead to a change in the competitive balance of the plant community due to inherent differences in plant resistance. Many plants have been shown to exhibit a wide range of sensitivity to enhanced UV-B radiation (for review see Teramura 1983). Since UV-B radiation can be considered as an environmental stress, any increase in UV irradiance could, in turn, lead to changes in competitive ability within plant communities through differential UV-B resistance of the competing species (Caldwell 1977). Competition could occur within the same species (intraspecific) or between different species (interspecific). Intraspecific competition becomes increasingly important in monospecific communities such as agricultural systems. On the other hand, in natural ecosystems with high species diversity, interspecific competition predominates. In agricultural systems interspecific competition could also be important between crops and weed species.

Gold and Caldwell (1983) studied intraspecific competition in wheat (*Triticum aestivum* L.), wild oats (*Avena fatua* L.), and goat grass (*Aegilops cylindrica* Host) at various planting densities. The study was conducted in the field at ambient levels of UV-B and those simulating a 16% ozone reduction (at Logan, Utah, 40° N, based on the generalized plant action spectrum). There were no significant differences in shoot biomass production at the various planting densities with enhanced UV-B radiation for all three species. This indicates that in these species, enhanced levels of UV-B radiation may be of little consequence in terms of intraspecific plant competition. Preliminary results (M. M. Caldwell, unpublished data, 1985) however, indicate that interspecific competition may be affected by enhanced levels of UV radiation. Enhanced levels of UV-B appeared to alter growth allocation patterns by inhibition of internode elongation in wild oat but not in wheat. This was reported to favor wheat in competition for available light. Whether similar responses occur among other agricultural crops is yet to be determined.

Solar UV exclusion studies in West Germany by Bruzek (cited in Gold and Caldwell 1983) with two pairs of naturally competing species show large differences in response to present levels of ambient solar UV radiation. In a *Fraxinus excelsior*/*Carpinus betulus* species pairing, reduction in shoot biomass with solar UV radiation was 42-14%, respectively, while in *Rumex obtusifolius*/*R. alpinus*, it was 10% and 24%, respectively. This suggests that

current levels of UV radiation are partly responsible for interspecific competition among various native plant species.

Very few studies have addressed interspecific competition under enhanced UV-B radiation. Fox and Caldwell (1978) and Gold and Caldwell (1983) examined the effects of enhanced UV-B radiation on the competitive interaction of nine groups of field grown competing pairs from three plant associations: agricultural crops and associated weeds, montane forage crops, and disturbed weedy associates. The results are summarized in Table 22.

To measure the competitive ability of one species when grown in mixture with a second species, relative crowding coefficients (RCC) were used. An RCC of 1.0 indicates that both species have a similar competitive ability. Species 1 has a competitive advantage when the RCC is greater than 1.0; species 2 has the advantage when the RCC is less than 1.0. As shown in Table 22, the RCCs based upon total above ground biomass indicate that there was a significant shift in the competitive balance in four of the species pairs: *Medicago sativa*/*Amaranthus retroflexus*; *Triticum aestivum*/*Avena fatua*; *Triticum aestivum*/*Aegilops cylindrica*; *Geum macrophyllum*/*Poa pratensis*. *Amaranthus* was more competitive under ambient UV conditions, while *Medicago* exhibited the competitive advantage under enhanced UV-B radiation. In *Triticum* grown under a simulated 16% ozone reduction, there was no significant difference in competitive ability with *Avena* but under a 40% ozone reduction, *Triticum* had a competitive advantage over *Avena*. However, in the previous year the competitive balance was found to be just the opposite, in favor of *Avena*. It was suggested that this difference was due to a late planting, which resulted in great water and temperature stresses during seedling development (Gold and Caldwell 1983). Between *Triticum* and *Aegilops* the competitive balance was shifted in favor of *Triticum* under enhanced UV-B radiation. Similarly, *Geum* had the competitive advantage over *Poa* under ambient conditions, but under enhanced UV-B radiation, the balance was shifted in the opposite direction.

Results also show that the extent of dominance can vary with UV-B irradiance. In the *Setaria glauca*/*Trifolium pratense* pairing, *Setaria* was dominant both under ambient and enhanced UV-B levels, but under enhanced levels the degree of dominance was expanded to a much greater extent. On the other hand, in the *Bromus tectorum*/*Alyssum alyssoides* pairing, although *Bromus* was dominant under both ambient and enhanced UV-B levels, this dominance was greatly reduced with enhanced UV-B radiation. These conclusions were all based on vegetative biomass since results on reproductive biomass, have not yet been made available. However, Gold and Caldwell (1983) report from preliminary field data that the competitive ability of wheat, based on seed biomass, increased relative to wild oats under enhanced UV-B radiation.

Combined, these results clearly demonstrate that enhanced levels of UV-B radiation can alter the competitive interactions of some species pairs. The competitive advantage of one species over the other depends upon the species pairing and the level of UV-B irradiation. Among the agricultural crops studied, *Medicago sativa* was more affected while *Triticum aestivum* was less affected by weed competition under enhanced UV-B radiation. Since there are a large number of weeds typically associated with various crop plants, the

Table 22. Relative Crowding Coefficients Based Upon Shoot Biomass Under Ambient and Enhanced Levels of UV-B Radiation. Enhanced UV-B Was Supplied Via Filtered (Kodacel TA 401) FS-40 Sunlamps. Data from Gold and Caldwell (1983) and Fox and Caldwell (1978).

Plant Association	Competing Species Pair		Simulated Ozone Depletion (%) <u>b/</u>	Relative Crowding <u>a/</u> Coefficient	
	Species 1	Species 2		Ambient UV	Enhanced UV <u>c/</u>
Agricultural crops and associated weed species	Alyssum alyssoides	Pisum sativum	40	0.34	0.25
	Amaranthus retroflexus	Medicago sativa	40	3.56	0.73*
	Amaranthus retroflexus	Allium cepa	40	1.89	2.01
	Setaria glauca	Trifolium pratense	40	2.06	18.74
	Triticum aestivum	Avena fatua	16	1.08	1.28
	Triticum aestivum	Avena fatua	40	1.08	1.69*
	Triticum aestivum	Aegilops cylindrica	16	0.48	1.57*
Montane forage species	Poa pratensis	Geum macrophyllum	40	0.85	2.28*
Disturbed area weedy associates	Bromus tectorum	Alyssum alyssoides	40	6.35	1.63
	Plantago patagonica	Lepidium perfoliatum	40	0.75	0.68

a/ Relative crowding coefficient of 0 means neither species has competitive advantage, more than 1 means species 1 has competitive advantage, less than 1 means species 2 has advantage.

b/ Simulated ozone depletion based upon generalized plant action spectrum (Caldwell 1971), calculated at Logan, UT (40°N).

c/ Asterisk denotes a significant difference (P less than 0.05) between control and enhanced UV treatment.

impact of enhanced levels of UV-B radiation upon agricultural systems is quite complex, but could potentially have serious consequences if weeds have a competitive advantage over crop plants. Total harvestable yield, as well as its quality, can be altered by the presence of weeds (Bell and Nalewaja 1968, McWhorter and Patterson 1980), even in the absence of UV.

Interspecific competition in natural plant communities even under current ambient UV-B radiation levels has rarely been documented through experimentation. Results of Caldwell and co-workers indicate that interspecific competition can be affected by enhanced levels of UV-B radiation. Thus the relative species composition of many natural plant communities could possibly change as a consequence of increased levels of UV-B radiation.

Caldwell (1977) suggested that because of the subtle nature of UV-B radiation stress, an enhancement of solar UV-B radiation may more likely alter the competitive balance of plants rather than directly affect ecosystem primary productivity. The results of Gold and Caldwell (1983) and Fox and Caldwell (1978) support this hypothesis. Except for the *Pisum sativum*/*Alyssum alyssoides* species pair, total productivity of each species pair was never significantly affected under enhanced UV-B radiation compared with ambient-grown controls. In contrast, the results of several field studies have demonstrated that total harvestable yield may be directly affected by UV-B radiation in agricultural systems (see Section 3.A, Direct Effects on Total Yield).

Because of the shifts in competitive balance reported here, increasing solar UV-B radiation could pose a considerable risk both to agricultural, as well as to natural, ecosystems. In agricultural systems, any shift toward increasing weed competitiveness would inevitably be detrimental in an economic sense, resulting in the need to increase tilling and/or herbicide application. Without such measures, an increase in weed occurrence may result in reductions in actual harvestable crop yields, a lowering in crop quality, or an alteration in disease or pest sensitivity. The apparent interactions of competitive balance with other commonly experienced environmental stresses, such as water and temperature stress, make it difficult to ascertain even the magnitude of the risk. Clearly, more experimental data is needed in this area.

Changes in the competitive balance of native species could also have profound effects on the structure and function of natural ecosystems. Presumably, the more UV-B-tolerant species would proliferate at the expense of the sensitive ones. Even very subtle differences in sensitivity could result in large changes in species composition over time and possibly affect ecosystem function. Again, because of the total lack of experimental evidence, the uncertainty is high; however, in light of the importance of this question, the risks are considerable.

### **3.E. Risks to yield due to changes in pollination and flowering**

It would seem that the reproductive tissues of plants whose pollination and subsequent fertilization take place during the day with flowers fully open would receive an appreciable UV-B dose. However, ovules enclosed in the ovary are well protected against UV-B radiation, and, therefore, female reproductive structures would not likely be affected. Flint and Caldwell (1983) have shown



in six plant species that the anther wall filters out over 98% of the incident UV-B radiation. Therefore, before anther dehiscence, pollen is also well protected. In-vitro experiments with pollen from numerous species demonstrate that UV-B radiation can inhibit pollen germination (Table 23). Sensitivity varies among species but even relatively low levels of UV-B radiation can inhibit germination in-vitro. Supported by other published results, Flint and Caldwell (1984) speculate that pollen shed in the binucleate condition would be more susceptible to UV-B radiation damage than pollen shed in the trinucleate condition. This speculation is based on the knowledge that the time course of germination and penetration of the stigma is more rapid in trinucleate species, and, thus, these would be less exposed to a UV-B radiation environment. Whether inhibition of pollen germination does occur under in-vivo conditions is yet to be determined.

In nine plant species, Southworth (1969) found UV-absorbing compounds in the wall of pollen, with a maximum absorbance in the UV-B range. The proposed role of pollen pigments also includes screening from UV radiation (Stanley and Linskens 1974). Furthermore, studies on the UV absorption profiles of stigmatic surfaces and exudates of many species show one or more peaks in the UV-B region (Martin 1970, Martin and Brewbaker 1971). Therefore, under natural conditions, the effectiveness of UV-B may be minimal because of UV-absorbing pigments in the anther and pollen walls. Upon deposition over the stigmatic surface, pollen would further be protected from UV-B radiation if the surface has exudates, since these often contain UV-absorbing compounds. On dry stigmatic surfaces, UV-B radiation may still have only minor effects, especially in trinucleate pollen because of the short time between germination and penetration. Furthermore, pollen absorption by the stigmatic surface also reduces its exposure. Although no direct experimental evidence is available to support or refute the hypothesis proposed by Flint and Caldwell (1984), results from various field experiments do not substantiate a meaningful change in grain yield or seed set under enhanced UV-B radiation.

Flint and Caldwell (1984) reported that maximum levels of solar UV-B radiation found in temperate latitudes were insufficient to inhibit pollen germination in-vitro, but that the two- to three-fold greater UV-B irradiance incident at high elevation, low latitude environments is effective in partially inhibiting germination in three of the four species they examined. This raises the question, then, whether pollen from tropical or subtropical species respond similarly or whether it is inherently more resistant to the greater, naturally occurring levels of UV-B radiation. Currently, no experimental evidence exists to help resolve this question. Overall, it appears that pollination at temperate latitudes may be little affected by the present projections for increases in solar UV radiation. However, there is considerable uncertainty with regard to risks to yield due to UV-mediated changes in pollination in tropical highlands. Intuitively, one might anticipate evolutionary adaptations which would protect the pollen of tropical species from the proportionally greater UV doses received in such environments. Despite its potential importance, however, the void of information available makes it impossible to assess this question fully at the present.

Table 23. Summary of UV-B Effect on In-Vitro Pollen Germination

Species	Irradiance* -2 mW/m <sup>2</sup> UV-B BE	Duration (hours)	Germination Inhibition (%)	Reference
Petunia hybrida	67	1.0	65	
Vicia villosa	67	1.0	65	Campbell et al. (1975)
Tradescantia Clone 4430	67	1.0	23	
Tradescantia Clone 4430	67	1.5	44	
Clone 02	67	1.5	12	Chang and Campbell (1976)
Brassica oleracea	54	2.5	28	
Cleome lutea	56	3.5	28	Caldwell et al. (1979)
Papaver sp	56	3.5	41	
Papaver rhoeas	35	3.0	3	
	60	3.0	35	
	68	2.0	26	
	137	3.0	52	Flint and Caldwell (1984)
	170	3.0	52	
Cleome lutea	40	3.0	2	
	60	3.3	33	
Geranium viscosissium	73	3.0	20	
Scrophularia peregrina	73	3.0	53	

\* Biologically effective UV-B weighted according to the plant effective action spectrum (Caldwell et al., 1979)

During the early part of this century numerous studies on the effects of solar UV radiation were conducted using window glass to filter out UV radiation (see reviews by Popp and Brown 1936; Caldwell 1971). The results from these studies indicated an inhibition of flowering by solar ultraviolet radiation. However, these experiments were generally executed with insufficient sample sizes and failed to isolate ultraviolet irradiation as the single contributing factor causing the difference in flowering. For instance, Caldwell (1968) has shown that leaf temperatures under window glass are markedly higher than under screen filters. Such changes in temperature alone are generally sufficient to alter the induction of flowering (Zeevaart 1976).

A summary of results from recent experiments under similar microclimatic conditions is presented in Table 24. Results of Kasperbauer and Loomis (1965) studying *Melilotus* and Caldwell (1968) with *Trifolium dasyphyllum* show an increase in flowering with the exclusion of solar ultraviolet radiation using greenhouse glass or Mylar filters. A growth chamber study by Klein et al. (1965) incorporating primarily UV-A radiation also shows an increase in the number of flowers produced in marigold by the exclusion of ultraviolet radiation. Similarly, greenhouse trials on beans and peas also show an inhibition of flowering and decrease in flower number due to UV-B radiation (Biggs and Basiouny 1975).

However, field studies providing enhanced levels of ultraviolet radiation using unfiltered sunlamps (which emit both UV-B and UV-C), produce no significant effects on flower number or date of flowering in marigold and tomatoes, tasseling in maize, or heading in sorghum (Hart et al. 1975). Biggs and Kossuth (1978), on the other hand, found an increase in flower number in potatoes at peak flowering in UV-B irradiated plants. However, the duration of flowering was longer under ambient levels of UV-B irradiance. In contrast, the number of flowers was significantly reduced in tomatoes after UV-B irradiation. Although these various observations apparently suggest changes in flowering which correlate with ultraviolet radiation, whether this would lead to an appreciable affect in harvestable yield has not been fully investigated. Biggs and Kossuth (1978) found a stimulation of flowering and an increase in tuber weight (grade A large) in potatoes with UV-B radiation, while UV-B induced inhibition of flowering in tomatoes resulted in reductions in fruit weight of 11 different maturity classes.

These results demonstrate that UV-B radiation can have both inhibitory and stimulatory effects on flowering, depending on the plant species, growth conditions and other factors. Whether UV-B radiation directly influences flowering events or plays an indirect role through changes in photosynthate reserves is not yet known. Presently, no clear trends emerge on the effects of UV-B radiation on flowering. Therefore, there is a high degree of uncertainty concerning the risk to yield due to a change in the timing of flowering. This uncertainty is primarily due to the paucity of experimental evidence available at this time. Whether alterations in flowering will lead to changes in harvestable yield still awaits further experimentation.

### **3.F Risks to yield due to structural plant changes affecting harvestability**

At present, no experimental study has directly addressed the question whether enhanced levels of UV-B radiation will alter the harvestability of

Table 24. Summary of UV Effects on Flowering

Plant Species	Growth Condition <u>a</u> /	Irradiation System	Conclusions	Reference
Melilotus	G.H.	unfiltered G.E. sunlamp and glass filtered	inflo. no. declined under unfiltered, but increased under glass	Kasperbauer and Loomis (1965)
	G.H.&F	none in G.H. ambient in F	flowered all season in G.H., decreased with season in field	Kasperbauer and Loomis (1965)
Trifolium dasyphyllum	F	ambient filtered with Mylar or Polyvinyl fluoride	increased flowering under Mylar	Caldwell (1968)
Kobresia myosuriodes	F	same	no sign. diff, but a trend of increased flowering under Mylar	
Carex rupestris	F	same	flowering under Mylar	
Geum rossii	F	same	same	
Oreoxis alpina	F	same	same	
Tagetes	G.C.	unfiltered black-light <u>b</u> /	exclusion of UV increased no. flower buds by 80% addition of UV increased no. flowers by 12%	Klein et al. (1965)
	F	unfiltered FS-40	no sign. effect	Hart et al. (1975)
Petunia	F	same	no sign. effect	
Zea mays	F	same	no effect on tasseling	
Sorghum bicolor	F	same	no effect on heading	

Table 24. Summary of UV Effects on Flowering (continued)

Plant Species	Growth Condition <u>a/</u>	Irradiation System	Conclusions	Reference
Phaseolus vulgaris	G.C.	Mylar and CA filtered FS-40	UV delayed flowering, no. and size of flowers	Biggs and Basiouny (1975)
Pisum sativus	G.C.	same	same	
Solanum tuberosum	F	same	UV decreased flowering duration increased no. open flowers at peak flowering	Biggs and Kossuth (1978)
Lycopersicon esculentum	F	same	UV decreased no. flowers on a single sample date	
Glycine max	G.H.	Mylar and CA filtered FS-40	no difference	Murali and Teramura (unpublished)

a/ GH = greenhouse, GC = growth chamber, F = field.

b/ 70% of radiation was between 355-380 nm (UV-A).

field crops. However, from morphometric changes reported in the literature, some speculations could be made. These speculations warrant caution because they represent only potential and not actual circumstances.

Crop harvestability is dependent upon crop architecture, time, and mode of harvesting. Crop architecture can be broadly grouped into 1) row type (e.g., cereals), 2) bushy (e.g., beans and tomatoes), and 3) trees. Crops are harvested either during final maturity as in cereals and legumes or at regular intervals as in alfalfa or other forage crops or fruits. Harvesting can be performed either manually or mechanically, or both. Changes in the harvestability of five crops are reported here as representative of potential scenarios.

Case 1, cereals (row crop). Harvestability of cereal crops, either mechanically or manually, depends upon the occurrence and extent of lodging. Losses would be heavy if there is a high degree of lodging, especially when harvested mechanically since no efficient mechanism for lifting plants without shattering grains has been developed. Most modern cultivars are highly resistant to lodging because of short and sturdy culms. However, under high sowing densities or excessive nitrogen supply, coupled with ample soil moisture, these cultivars tend to grow taller and occasionally lodge severely during storms. Furthermore, culms can break in strong winds resulting in goosenecking of panicles. Enhanced levels of UV-B radiation generally reduces plant height in cereals (Table 25). Such an effect would have a positive effect on the harvestability of cereals by decreasing their susceptibility to lodging.

Case 2, tomatoes (bushy crop). Tomatoes are grown either for fresh market or processing. The former is mainly of indeterminate and the latter of determinate type. In indeterminate tomatoes, plants are pruned to remove the lateral buds/branches and staked because of their viney nature. These are highly labor-intensive operations. Hart et al. (1975) reported an inhibition of branching with no reduction in fruit number or size due to enhanced UV-B irradiance in field-grown tomatoes (cultivar Fire ball). This suggests that increasing UV-B levels could potentially have a favorable effect on tomato culture by minimizing the labor requirement for pruning. Presently, it is not known whether pruning or UV-induced inhibition of lateral branching will result in greater yields due to reallocation of resources to the main stem. Larger fruits may possibly be produced by the removal of lateral branches due to the diversion of photosynthate. Another advantage of UV-induced inhibition of lateral branching concerns the earliness of ripening. For instance, it is known that with fewer branches, ripening occurs earlier in indeterminate types. Thus, early-season market requirements can be met by the reduction of branching. An increase in UV-B radiation could also favor a longer period of staggered production due to early ripening and thus an improved distribution of fruit for harvesting. At higher latitudes, where the growing season is shorter, earliness in ripening can be an advantage to a grower.

Tomatoes grown for processing are primarily of the determinate type. Because of their uniform ripening they can be mechanically harvested. In mechanical harvesting, one of the prerequisite characteristics is the ease of separation of fruits from stems and leaves. Fruits can be generally separated more easily when there are fewer branches, *ceteris paribus*. Thus, UV-mediated inhibition of branching could also increase mechanical harvestability of tomatoes.

Table 25. Summary of UV-B Effects on Plant Height of Cereals

Crop	Growth Condition	UV-B Irradiance	% Relative Change in Plant Height	References
Sweet corn ( <i>Zea mays</i> )	Field	1.0-1.7 UV-B Beltsville Sun Equivalents Unfiltered FS-40 Sunlamps	+14 to -3	Ambler et al. (1978)
Sorghum ( <i>Sorghum vulgare</i> )			- 1 to +3	Ambler et al. (1978)
Sweet corn ( <i>Zea mays</i> )	Greenhouse	131-225 mWm <sup>-2</sup> UV-B <sub>BE</sub> (plant)	-15 to -22	Allen et al. (1977)
Wheat ( <i>Triticum aestivum</i> )	Growth Chamber	0.5 to 2.0 UV-B Sun Equivalents	-5 to -22	Biggs and Kossuth (1978)
Barley ( <i>Hordeum vulgare</i> )	Growth Chamber	0.5 to 2.0 UV-B Sun Equivalents	-14 to -22	Biggs and Kossuth (1978)
Corn ( <i>Zea mays</i> )	Growth Chamber	0.5 to 2.0 UV-B Sun Equivalents	-14 to -28	Biggs and Kossuth (1978)
Millet ( <i>Pennisetum glaucum</i> )	Growth Chamber	0.5 to 2.0 UV-B Sun Equivalents	-13 to -20	Biggs and Kossuth (1978)
Oats ( <i>Avena sativa</i> )	Growth Chamber	0.5 to 2.0 UV-B Sun Equivalents	-9	Biggs and Kossuth (1978)
Rice ( <i>Oryza sativa</i> )	Growth Chamber	0.5 to 2.0 UV-B Sun Equivalents	-4 to -13	Biggs and Kossuth (1978)
Rye ( <i>Secale cereale</i> )	Growth Chamber	0.5 to 2.0 UV-B Sun Equivalents	-21	Biggs and Kossuth (1978)
Corn ( <i>Zea mays</i> )	Field	8-16% O <sub>3</sub> red.	+1 to +5	Biggs et al. (1984)
Barley ( <i>Hordeum vulgare</i> )	Growth Chamber	1060-1760 -2 <sup>-1</sup> Jm <sup>-1</sup> -day UVB <sub>BE</sub> (Plant)	-1 to -12	Dumpert (1983)
Wheat ( <i>Triticum aestivum</i> )	Growth Chamber	1060-1760 -2 <sup>-1</sup> Jm <sup>-1</sup> -day UVB <sub>BE</sub> (Plant)	-1 to -2	Dumpert (1983)

Case 3, cotton (bushy crop). Grading the quality of cotton harvested mechanically or manually depends on the degree of contamination, especially from dried leaves. Although defoliants are used before mechanical picking, the extent of leafiness still can have a direct bearing upon harvestability. Intuitively, the more leafy the crop, the greater the probability of contamination. Biggs and Kossuth (1978) found a significant increase (9 to 16%) in leaf area produced under enhanced levels of UV-B radiation in cotton (*Gossipium hirsutum*). Unfortunately, they did not evaluate cotton yield or quality to determine whether the increase in leafiness had any deleterious effects.

Case 4, tobacco (bushy crop). The mechanical harvesters presently designed and used for tobacco are more effective in cultivars with leaves oriented in an upright fashion. Since larger leaves tend to droop, cultivars with smaller leaves are better suited for mechanical harvesting. To date, there are no experimental data on morphological changes arising from enhanced levels of UV-B radiation in tobacco. However, studies conducted with numerous crop plants show a general reduction in leaf area (Teramura 1983). On the other hand, an increase in leaf area as found in cotton (Biggs and Kossuth 1978), could pose some difficulty for mechanical harvesting.

Case 5, fruits (tree crop). Phytohormones such as ABA and ethylene regulate fruit abscission. Biggs and Kossuth (1978) reported an increase in both ABA and ethylene with enhanced levels of UV-B radiation in bean plants. Currently, it is not known whether such a response is general in nature and elicited in tree fruits. If so, there is the possibility that fruit may be abscised prior to reaching maturity, resulting in considerable economic losses.

#### 4. SUMMARY AND CONCLUSIONS

Global UV-B radiation varies diurnally and seasonally because of changes in solar angle, stratospheric ozone concentration, degree of cloud cover, etc. Presently, most investigators evaluate the effects of UV-B radiation using a constant UV-B supplied via simple lamp systems without considering these temporal changes in UV-B irradiation. This results in an oversupplementation of UV during periods of low solar angle (morning and afternoons) and during overcast skies.

The effects of UV-B radiation in producing a plant response is highly wavelength dependent. In evaluating the effectiveness of UV-B radiation, more than 10 action spectra have been developed and used by various investigators. Since these action spectra vary tremendously many of the experimental data from various UV-B studies are not directly comparable. Thus, a realistic action spectrum developed under more natural conditions must be developed and used in all future experiments.

There are 10 major terrestrial plant ecosystems in the world and these include 314 plant families. The effects of enhanced levels of UV-B have been studied in only four of these ecosystems and in only 6% of the plant families. UV effects have been examined in only about a third of the plant growth forms and in many, such as vines, epiphytes, small woody shrubs, etc., virtually no data exists. Most of our knowledge of UV effects is derived from studies focused upon agricultural crops, yet crop yield has been evaluated in only 22 species from 7 plant families. Overall, very little information is available



on the effectiveness of UV-B radiation on other economically important plants such as trees and forage grasslands and especially on native plant species. To adequately address the question of what potential impacts enhanced levels of UV-B radiation will have on global terrestrial plant communities and ecosystems, many unrealistic assumptions must be made. For example, to assess the potential impacts on forest communities, we must assume that perennial woody trees and shrubs respond similarly to annual agricultural crops. Clearly more data would be needed before any attempt for realistic projections on a global scale could be made.

Plant responses to increased levels of UV-B radiation vary markedly both among (interspecific) and within (intraspecific) plant species. At present, the bases for these inherent differences have not yet been well documented. There are three general categories of UV-protective mechanisms which may be involved in producing this variation in responses. The first includes repair mechanisms, such as photoreactivation, which is an enzyme mediated, light-activated process. Although not specifically demonstrated in plant tissues, various experimental results suggests it is a widespread phenomenon. Excision repair is the process whereby potentially deleterious photoproducts of UV absorption are removed and replaced by new, correct DNA sequences. This is clearly demonstrated and is a widespread phenomenon in plants. Postreplication repair involves the replication and combination of intact DNA strands over damaged ones, but is yet unknown in plant tissues.

The second category of protective mechanisms are those that tend to minimize the damaging effects of UV-B radiation. Probably the most important of these is growth delay, which allows time for other repair mechanisms to correct the damage. The last category involves those which effectively reduce the amount of UV-B radiation reaching sensitive targets. The most widespread mechanism in plants is probably the selective absorption by UV-absorbing pigments such as flavonoids in outer tissue layers. Some studies show that despite a large increase in flavonoids, the photosynthetic machinery is still adversely affected by UV-B radiation. Therefore the inherent inter- and intraspecific differences in UV-B sensitivity are probably the product of a number of natural UV protective mechanisms acting in concert within the plant. More information is critical to refine our understanding of natural plant protective mechanisms which may potentially help compensate damage arising due to the anticipated increase in solar UV-B radiation.

Large intraspecific differences in UV-B sensitivity have been reported, which are not merely the result of gross morphological or physiological differences, as might commonly occur interspecifically. Crop breeding could be used as a tool to minimize the deleterious effects of UV-B radiation if a thorough understanding of the genetic bases for these differences were understood. Despite the evidence of UV-tolerant cultivars supporting the notion that crop breeding may limit the deleterious impacts of enhanced solar UV-B radiation, a large degree of uncertainty still remains in the absence of any information on the genetic bases for these differences.

Much of our understanding of the effects of UV-B radiation on plants is derived from studies conducted under artificial growth conditions (growth chamber or greenhouse) which neither quantitatively nor qualitatively resemble field conditions. Of utmost concern is that plants are apparently more sensitive to a given UV-B dose in artificial growth conditions compared with field conditions. The theoretical basis for increased susceptibility is that

under artificial conditions only a single factor is generally manipulated, while all other factors are kept constant or optimized for growth. Under field conditions, however, plants typically experience multiple stresses (water, nutrients, etc.) simultaneously. Few studies have examined the interaction between other commonly experienced stresses and UV-B radiation. Both water and nutrient stresses apparently increase plant tolerance to UV-B radiation by stimulating the production of UV screening chemicals. Artificial growth environments can provide valuable information on the interaction between UV-B radiation and other environmental factors; however, they cannot be used in place of actual field validation studies where a host of complex natural interactions occur. It is concluded that when extrapolations from controlled environments are made into the field, they must be done so with extreme caution. At best, general trends may be implied, but specific or quantitative extrapolations do not yet seem plausible.

Atmospheric CO<sub>2</sub> concentration has been steadily increasing over the centuries, but at an alarmingly faster rate during the past two decades. To date, no information is available on the effects of UV-B radiation under increased atmospheric CO<sub>2</sub> concentrations; however, some speculations could be made. In general, enhanced levels of UV-B radiation has a negative effect, while CO<sub>2</sub> has a positive effect, on the growth and development of plants. Since the positive effects of CO<sub>2</sub> are generally greater than the negative effects produced by UV-B irradiation, the combination of these two environmental changes might lead to a compensation of some of the deleterious, direct effects of UV-B radiation. Therefore, more subtle, indirect effects may be those most critically affected. Both UV-B and CO<sub>2</sub> have been shown to alter the competitive balance among various plant associations. Changes in competitive balance, especially in agricultural systems between crops and weeds could produce subtle, yet economically catastrophic changes. Shifts in competitive ability among native species could lead to changes in community composition and structure, with ultimate large-scale ecosystem modifications. Considering the lack of any experimental data on the actual interaction between UV-B and CO<sub>2</sub>, there is a high degree of uncertainty in the assessment of the possible global effects of enhanced levels of UV-B radiation in an elevated CO<sub>2</sub> atmosphere.

In all of the industrialized countries in the world, ground-level air pollution (oxides of nitrogen, sulphur dioxide, fluoride, and ozone) is rapidly increasing. In many cases these pollutants have already had detrimental effects on plant productivity. At present, no experimental data are available on the interactions between UV-B radiation and these various other air pollutants. However, since most air pollutants have deleterious effects on plants, it is anticipated that the effects of UV-B would be additive.

Only a handful of field studies have examined the effects of UV-B radiation on crop yield. Despite a broad range of experimental protocols and dosimetry, in nearly half of the plant species examined, UV-B radiation produced a deleterious effect on yield. Although reductions in yield were reported for some crops, this result should be evaluated with caution since most studies lasted for only a single growing season. Field studies conducted over several years show large annual variation in response. Only two studies have evaluated the effects of UV-B radiation on the quality of crop yield, and both reported reductions. Overall, UV-B radiation deleteriously affects both the quantity and quality of crop yield, but the magnitude of the effect is

highly variable from one year to another. Longer-term field studies are essential for realistic assessments of the impact of increased levels of solar UV-B radiation on the quantity and quality of global crop productivity.

Crop yield is also affected by factors such as the occurrence of pests and diseases, weeds, problems associated with pollination, etc. Several studies have specifically examined the effects of UV-B radiation on the severity of pest and disease incidence. Although some of these results suggest that UV-B can have potentially beneficial effects on pest control, these must be interpreted cautiously since the observation period was very short. The effects of UV-B radiation on plant diseases was equivocal, varying with pathogen, plant species, and cultivar. One study reported that UV-B radiation significantly reduced virus infection transmitted mechanically. However, virus or viroids transmitted through seeds, pollen, insects, or nematodes may not be as susceptible to UV-B radiation due to the additional cellular screening offered by the host tissue. UV-B radiation may further reduce yield by increasing the incidence of pests and diseases, or in other instances potentially have beneficial effects on pest and disease control. Lack of sufficient information leads to a high degree of uncertainty in the projection of the impact of enhanced solar UV-B radiation on pest and diseases.

Numerous agricultural and native plant species are differentially affected by UV-B radiation, which could ultimately lead to changes in the competitive balance within plant communities. In agricultural situations, there may be a shift in the competitive ability of weeds, resulting in the need for increased production costs (tillage, herbicides, etc.). Without such measures, an increase in weed competition would reduce the quantity and quality of yield. Once more, the lack of experimental evidence precludes more detailed assessment.

In-vitro experiments with pollen from numerous species show that even relatively low levels of UV-B radiation can inhibit pollen germination. However, whether a similar response occurs in-vivo has yet to be determined. Both the pollen wall and stigmatic surfaces have UV-absorbing pigments, thus under natural conditions the effectiveness of UV-B may be minimized. Observations from various field experiments do not indicate any substantial change in the seed set which would support this notion. Therefore, it appears that the projected increase in UV-B radiation may not affect pollination.

Only two field studies have investigated the effects of UV-B radiation on flowering. Based upon this limited information, UV-B may affect flowering in some plants, but possibly without any affect on yield. However, the absence of conclusive information makes it impossible to further assess the impact of UV-B radiation on pollination and flowering.

No experimental information is available on UV-induced structural changes which might affect the harvestability of field crops. However, on the basis of reported morphometric changes, some speculations were made on five crops. UV-B radiation may potentially have a beneficial effect by reducing the labor cost for pruning in some crops and stimulate ripening for early season market. UV-B radiation has been shown to increase leaf area in cotton, which may reduce cotton quality because of higher levels of contamination from dry leaves. In cereals, UV-B reduces internode length and thus the height of the plant. This may have a positive effect on the harvestability of cereals by decreasing their susceptibility to lodging. UV-B may also increase mechanical

harvesting efficiency in some crops by decreasing leaf area. It is reported that UV-B radiation increases both ABA and ethylene production in some plants. Since phytohormones regulate fruit abscission, UV-B radiation may result in considerable economic losses by abscising fruit prior to maturity. Overall, it appears that increased levels of UV-B may be beneficial to the harvestability of some crops, while others might be negatively affected.

## 5. RECOMMENDATIONS

A plethora of experimental approaches, equipment and dosimetry have been utilized in the numerous studies presented in various earlier sections. One major consequence of such experimental diversity is the difficulty in interpreting data for comparative purposes. In a worst-case example, consider the field studies conducted with unfiltered fluorescent sunlamps that emit short wavelength UV-C radiation. Caldwell (1977) calculated that even in the unlikely event of a catastrophic 90% stratospheric ozone depletion, almost no energy would be emitted at wavelengths shorter than 280 nm (in the UV-C waveband). Furthermore, evidence suggests that the effects of the UV-C waveband may differ both quantitatively and qualitatively from effects of UV-B radiation (Nachtwey 1975). Since unfiltered lamps emit energy both in UV-C and UV-B wavelengths, such studies have virtually no utility in estimating the potential impacts of increasing solar UV-B radiation reaching the earth's surface. To have any ecological relevance, UV lamps must be filtered to remove the UV-C component.

The most common UV sources used for plant effects research are the Philips TL 40/12 fluorescent sunlamps filtered with Schott cut-off absorption filters (WG series), used primarily by European investigators, and the Westinghouse FS-40 fluorescent sunlamp filtered with cellulose acetate plastic films used exclusively by U.S. investigators. The Philips lamps have a considerably greater UV emittance than the Westinghouse ones, and the two filtered lamp systems differ in spectral energy distribution (Caldwell et al. 1984). Therefore, it is crucial that the same weighting functions be used when comparing experiments using different UV irradiation systems. As the difference between spectral distributions increases (for example when comparing high- and low-pressure mercury vapor lamps) the choice of the action spectrum becomes more critical (see Appendix A, Action Spectra and their Key Role in Assessing Biological Consequences of Solar UV-B Radiation Change). Since FS-40 lamp output decreases rapidly (20%) during the first 100 hours of use, it is recommended that lamps be pre-aged prior to use (Teramura et al. 1980).

The UV-B irradiation emitted along the length of a fluorescent tube varies greatly. Maximum emittance occurs in the middle third of the lamp and this diminishes rapidly near the ends, where emittance may be only 50% of maximum. This can be graphically seen in Figure 4 showing the normalized irradiance 0.5 m beneath a Westinghouse FS-40 lamp array. The array consisted of six parallel lamps (shown by arrows), and measurements were made each 10 cm in a 2.3 square meter area directly beneath the lamps. Plants grown in the middle 0.6 m<sup>2</sup> of such an array receive a relatively uniform irradiance which varies by less than 10%. Therefore, it is recommended that lamps be oriented perpendicular to experimental plant rows, rather than in an end-to-end fashion. Although an end-to-end orientation is much more economical, plants beneath such an irradiation system would receive a highly variable UV dose, ultimately producing an appreciable degree of experimental error (in a

25	30	34	39	41	45	45	45	48	45	45	45	45	43	41	39	36	32	23
30	36	43	52	55	59	61	59	64	64	61	59	59	57	55	50	48	41	34
36	48	55	61	68	61	73	68	77	77	75	61	73	57	66	64	57	48	41
43	52	61	70	77	80	84	84	86	86	86	84	82	80	75	70	64	57	45
45	59	68	77	84	89	91	93	93	93	91	91	91	89	82	77	68	59	48
48	59	70	80	89	91	95	98	100	98	98	95	93	89	86	77	73	61	50
52	59	70	80	89	93	95	98	100	100	98	98	93	93	86	80	73	61	50
48	59	68	75	86	91	93	95	98	95	95	93	91	89	82	80	68	59	50
43	55	64	70	80	84	89	91	91	89	89	89	89	82	77	73	64	57	45
36	48	57	61	68	73	80	82	80	77	55	77	77	73	68	64	57	50	41
27	39	45	50	57	61	61	64	66	66	64	64	61	57	55	52	45	41	32
18	27	34	36	41	45	48	48	50	48	48	45	45	45	41	39	32	30	23

▲                                 ▲                                 ▲                                 ▲                                 ▲                                 ▲                                 ▲

**Fig. 4** Normalized irradiance 0.50m beneath a single UV-B lamp array. Measurements were made each 100 cm<sup>2</sup> with lamps positioned at 0.30m centers (actual lamp position indicated by arrows).

statistical sense). It is likely that the larger error associated with such a variable dose could mask some of the subtle UV-B radiation effects, and therefore not be a reliable test.

The level of visible radiation supplied during growth has profound effects on plant sensitivity to UV-B radiation (see Section 2.C, Issues Associated with the Extrapolation of Data from Controlled Environments into the Field). Therefore, caution must be exercised in controlled environment studies to maintain an adequate level of visible radiation. Since leaf anatomy and photosynthetic characteristics have been shown to be related to the daily integrated levels of visible radiation (Chabot et al. 1979, Nobel and Hartsock 1981), it is recommended that the daily dose of visible radiation be in an ecologically realistic range wherever possible.

In nearly all field experiments, supplemental UV-B radiation is provided as a squarewave, simply by turning lamps on or off with the use of timers. Natural solar UV irradiance, in contrast, gradually increases on a daily basis with a peak at solar noon that coincides with peak visible irradiances. Therefore under artificial lamps producing a squarewave function, proportionately more UV is provided during the periods of low solar altitudes (mornings and late afternoons) compared with natural solar UV. This results in a greater simulated ozone reduction during these periods. Of even greater concern, however, is that such a squarewave is generally supplied during cloudy and overcast skies, when the levels of ambient UV may be less than 50% of clear sky irradiances due to the absence of the direct beam component. During these periods, the lamps would supply a UV dose equivalent to a much greater ozone depletion than originally intended when the lamps were calibrated for clear sky conditions. More realistic field validations of anticipated ozone depletion may be made using a modulated lamp system as described by Caldwell et al. (1983b). Such a system would reduce the errors cited above by providing UV as a sinewave during clear sky conditions and modulate lamp output during cloudy or overcast skies. A further advantage in a modulated system would be a reduction in the frequency of filter changes necessary (currently once every 4-7 days for most investigators) since the system would correct for filter solarization. The disadvantage with such a system is the additional project cost. Estimates for building a modulated system range between \$1,000 to \$1,500 per unit (Caldwell personal communication), and one unit would be necessary to control an array of six lamps. In the field study conducted by Teramura (1981), 60 such modulated systems would be necessary. Despite the additional expense, such a refinement could greatly improve the field simulation and sensitivity of ongoing and future field validation studies. In light of the great risks posed to global crop yield and quality loss resulting from a projected increase in UV-B radiation reaching the earth's surface, such an investment seems well warranted and therefore highly recommended.

Instrumentation to measure UV-B radiation has essentially evolved along with project needs during the past decade. The current spectroradiometer used by U.S. scientists involved in plant effects research is the Optronics (Orlando, Florida) Model 742, with a double monochromator and dual holographic grating specifically designed to measure the UV spectral irradiance of sunlight. Although this instrument is excellent in laboratory situations, it is not ideally suited for field measurement. Several investigators have made some extensive modifications which have greatly improved its ability to function in the field. For instance, Caldwell (personal communication) has

installed a Peltier cooling device to keep the photomultiplier tube at a uniform temperature, enabling the spectroradiometer to operate in a temperature range typically found in the field (30-40°C). It is recommended that this equipment modification as well as others be made (perhaps in conjunction with Optronics) to improve the reliability of our field measurements.

The recommendations made above are suggestions which will help improve field experimental design and measurement and help limit extraneous variations which may mask any true UV-induced biological effects. More importantly, however, an adoption of standardized protocols and dosimetry will greatly aid in the interpretation and intercomparison of field collected data and provide a reliable basis from which to assess the potential impacts of stratospheric ozone depletion.

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**APPENDICES**

APPENDIX A

**ACTION SPECTRA AND THEIR KEY ROLE IN ASSESSING  
BIOLOGICAL CONSEQUENCES OF SOLAR UV-B RADIATION CHANGE**

By

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## Action Spectra and Their Key Role in Assessing Biological Consequences of Solar UV-B Radiation Change

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### ABSTRACT

Action spectra of UV damage to plants must be used as weighting functions to (1) evaluate the relative increase of solar UV radiation that would result from a decreased atmospheric ozone layer, the radiation amplification factor--RAF, (2) evaluate the existing natural gradients of solar UV irradiance on the earth, and (3) compare UV radiation from lamp systems in experiments with solar UV radiation in nature. Only if the relevant biological action spectra have certain characteristics is there a potential biological problem that would result from ozone reduction. Similarly the existence of a natural latitudinal solar UV gradient is dependent on action spectrum characteristics.

Several UV action spectra associated with different basic modes of damage to plant tissues all have the common characteristic of decreasing effect with increasing wavelength; however, the rate of decline varies considerably. Extrapolation from action spectra that have been measured on isolated organelles and microorganisms using monochromatic radiation to effects of polychromatic radiation on intact higher plants is precarious. Development of action spectra using polychromatic radiation and intact higher plant organs can yield spectra that are of more ecological relevance for weighting factors in assessment of the ozone reduction problem. An example of an action spectrum for photosynthetic inhibition developed with polychromatic radiation is provided in this chapter. This action spectrum has different characteristics, and results in a greater RAF than do action spectra for inhibition of a partial photosynthetic reaction, the Hill reaction, developed with isolated chloroplasts and photosynthetic bacteria. Circumstantial evidence from experiments with plants originating from different latitudes also supports the notion that action spectra with characteristics similar to that of the provisional spectrum, developed with polychromatic radiation, are appropriate. Further work with polychromatic radiation is encouraged.

There are two basic types of error that are associated with the use of action spectra in biological assessments of the ozone reduction problem, the RAF errors and the enhancement errors. The former are those associated with calculation of the RAF, and the latter are those derived from calculation of the UV radiation enhancement used in experiments with lamp systems. While the RAF errors are recognized, the enhancement errors have not been generally appreciated. An error analysis is presented showing that the

enhancement errors will typically be larger and in the opposite direction than the RAF errors. The enhancement error should be considerably less in field UV supplementation experiments than in most laboratory experiments which employ fluorescent lamps as the primary UV-B radiation source.

## INTRODUCTION

Traditionally, biological action spectra have been employed to elucidate photobiological mechanisms, and specifically to identify potential chromophores. Action spectra are usually assessed by evaluating biological responsiveness to monochromatic irradiation. In order to identify potential chromophores, there has been an emphasis on the fine structure of action spectra and little attention has been directed to the tails of these spectra.

In assessment of the consequences of solar UV-B radiation changes, action spectra serve a very different role. Weighting functions are derived from action spectra to assess the relative biological effectiveness of polychromatic irradiance. Spectral irradiance is weighted and then integrated over a waveband of interest, thus:

$$\text{effective irradiance} = \int I_{\lambda} E_{\lambda} d\lambda \quad (1)$$

where  $I_{\lambda}$  is the spectral irradiance, and  $E_{\lambda}$  is the relative effectiveness of irradiance at wavelength  $\lambda$  to elicit a particular biological response. The limits of the integration are prescribed by the wavelengths where either  $I_{\lambda}$  or  $E_{\lambda}$  approach zero.

Spectral irradiance and the action spectra can be expressed on either a photon or an energy basis. As units of effective irradiance it is most useful to speak of "weighted" or "effective" energy flux or photon flux density (e.g., effective  $W m^{-2}$  or effective moles photons  $m^{-2} s^{-1}$ ) and, of course, to specify the action spectrum used as a weighting function and the wavelength to which the spectrum is normalized. Special units analogous to units of illumination (e.g., lux) have been previously devised for effective UV radiation (such as sunburn units, E-viton and the Finsen for erythemally effective radiation (Robertson 1975; Luckiesh and Holladay 1933) and the G-viton for germicidal UV radiation (Luckiesh and Holladay 1933). However, unlike illumination where a standard spectral luminosity function has been well accepted, UV action spectra for various biological phenomena are continually being refined or abandoned in favor of new action spectra and, thus, either the units need to be redefined or new units described. Therefore, use of effective energy or photon flux with a specified action spectrum is quite preferable to the definition of new units.

The utility of weighting the UV irradiance and, thus, expressing biologically effective irradiance for the ozone reduction problem derives from the highly wavelength-specific absorption characteristics of atmospheric ozone and the wavelength specificity of biological action spectra in the UV-B waveband (National Academy of Sciences 1979; Nachtwey and Rundel 1982; Caldwell 1981). The expression of weighted effective irradiance is useful in addressing three basic issues:

(1) The degree to which biologically damaging solar UV irradiation is increased when atmospheric ozone decreases is very dependent on the action spectrum characteristics. The increment of biologically damaging solar irradiation resulting from a given level of ozone reduction for a specific set of conditions, is known as the radiation amplification factor, RAF (National Academy of Sciences 1979). Without calculation of an RAF, which takes the biological effectiveness of each wavelength into account, the increment of total solar UV-B flux resulting from ozone reduction is trivial, e.g., 1% increase of UV-B radiation for 16% ozone reduction for midday irradiance in the summer at temperate latitudes (Caldwell 1981). The increase of solar UV-B irradiation as a function of ozone reduction only becomes significant when the biological effectiveness of this radiation is calculated and the action spectrum for this calculation has certain characteristics. By the same token, if the action spectrum of a particular biological phenomenon does not exhibit the appropriate characteristics, the RAF will be very small and this phenomenon can be eliminated from concern with respect to the consequences of ozone reduction without the necessity of dose-response studies.

(2) The steepness of the natural latitudinal gradient of solar UV-B irradiance that currently exists on the Earth's surface should also be evaluated in terms of potential biological effectiveness. The natural gradient of UV-B radiation serves as a basis for study of organism response to solar UV-B radiation and can provide insight into potential consequences of ozone reduction. This gradient has been used most frequently in the analysis of human skin cancer incidence; however, study of plant adaptation to UV-B radiation at different latitudes can also be instructive (e.g., Caldwell et al. 1982; Robberecht et al. 1980). As is the case with ozone reduction, without taking biological effectiveness of solar UV-B irradiation into account, the natural latitudinal gradient of solar UV-B radiation is virtually nonexistent (Caldwell 1981).

(3) Since spectral irradiance received from commonly-used lamp systems for UV-B studies does not match that of solar irradiance, it is only possible to draw comparisons by calculating "biologically effective" radiation using action spectra as weighting functions. Characteristics of action spectra will thus dictate the amount of radiant flux delivered by lamp systems in experiments designed to evaluate potential consequences of ozone reduction under different conditions.

This chapter will (1) review a few action spectra illustrating different fundamental mechanisms of UV-B damage in plant cells, (2) discuss the use of polychromatic radiation in determining action spectra and illustrate this with a new action spectrum for photosynthetic inhibition, (3) show the nature of radiation amplification factors that result from action spectra of different characteristics, (4) briefly discuss the implications of action spectra for the natural latitudinal gradient of solar UV-B radiation, and (5) develop an error analysis of the types and magnitude of errors that might be encountered in biological assessments by assuming an improper action spectrum.

## ANALYSIS

## Modes of Damage and Their Spectra

Ultraviolet radiation can damage plant cells by several basic mechanisms and these pathways of damage likely involve several different chromophores. To illustrate the diversity of damage pathways, several action spectra are depicted in Fig. 1. In each case the reaction is identified with damage to a specific entity or process in the cell. However, this does not mean that the entity damaged is necessarily the primary chromophore (Peak and Peak 1983). All spectra are normalized to 300 nm. Though these spectra

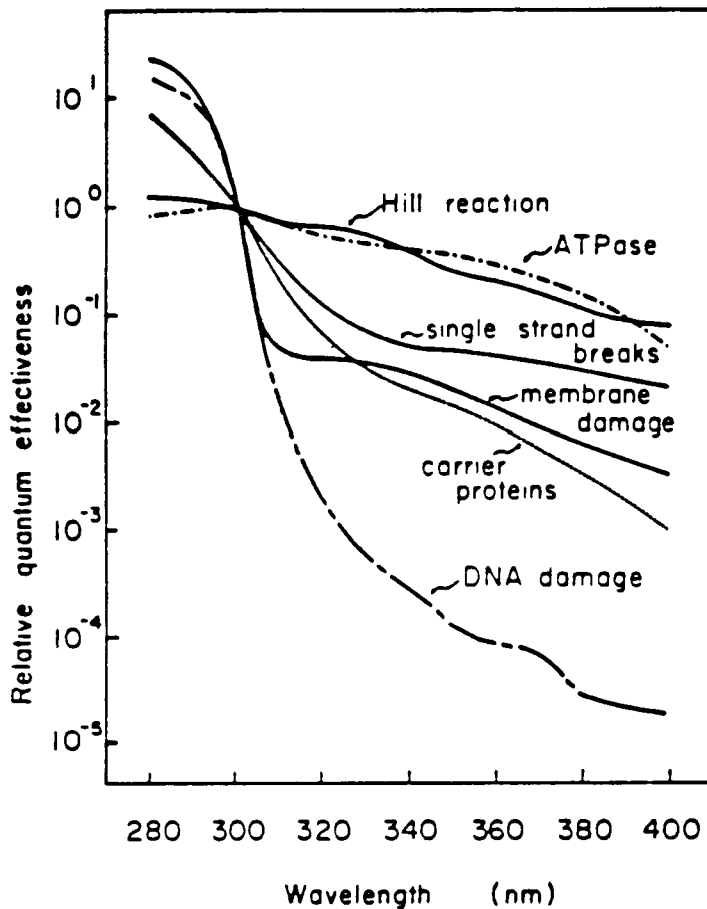


Fig. 1. Ultraviolet action spectra representing basic modes of damage to plant tissues. The spectra were all developed with monochromatic radiation and are plotted on a quantum effectiveness basis relative to 300 nm. These include inhibition of Hill reaction activity in isolated chloroplasts of spinach (Jones and Kok 1966), inhibition of adenosine triphosphatase (ATPase) from plasma membranes of *Rosa damascena* (Imbrie and Murphy 1982), induction of single strand breaks of *Bacillus subtilis* DNA (Peak and Peak 1982), lethality of stationary phase cells of *E. coli* associated with cell membrane damage (Kelland et al. 1983), inhibition of alanine uptake in *E. coli* linked to inactivation of carrier proteins (Sharma and Jagger 1981), and inactivation of stationary phase cells in *E. coli* associated with nucleic acid damage (Webb 1977).



represent different basic pathways of damage, and in many cases presumably very different chromophores, all have the common property of decreasing effect as wavelength increases. These spectra have been developed in the normal manner using monochromatic radiation and in several cases have been pursued through several orders of magnitude. If these were to be plotted with a linear ordinate, the differences in these spectra would be much less apparent. Nevertheless, as will be discussed subsequently, if these spectra are to be used as weighting factors for solar UV radiation, which increases by orders of magnitude with increasing wavelength, the differences in slopes of these action spectra are of key importance. These spectra have been determined with isolated organelles, membranes, or microorganisms, but none involved intact higher plants.

#### Complications: Intact Higher Plants and Polychromatic Radiation

Since the spectra illustrated in Fig. 1 differ greatly in their decline with increasing wavelength, it is important to know which of these primary damage mechanisms are the most important for intact higher plants exposed to solar radiation. This is not an easily answered question. One would need to know (1) the basic sensitivity of the respective targets (e.g., DNA, membranes, Photosystem II of photosynthesis, etc.) for the higher plant species in question, (2) how well shielded these targets are within the plant organ (i.e., the effective spectral fluence reaching the target), (3) to what extent reciprocity would apply, and (4) if radiation at different wavelengths when applied simultaneously and in proportion to their occurrence in sunlight would have strictly additive effects, as predicted by the action spectrum, or whether these effects would be positively or negatively synergistic. Addressing these several issues is hardly a trivial undertaking and satisfactory answers are not likely to be quickly forthcoming. For example, as to the question of synergistic effects of radiation at different wavelengths, much is known about mechanisms of UV radiation effects on nucleic acids and yet it is still difficult to quantitatively predict synergistic effects in higher plants. From in vitro studies and from in vivo experiments with microorganisms, it is clear that there are qualitative differences between UV-B and UV-A damaging photoreactions (Peak and Peak 1983): UV-A radiation can drive photorepair of UV-B-induced damage (Jagger 1981), UV-B radiation can induce other repair systems which can repair at least a fraction of the UV damage (Menezes and Tyrrell 1982), UV-A radiation can cause growth delay in bacteria which allows more time for dark repair systems to operate (Jagger 1981), and, finally, UV radiation at high fluence rates can damage UV repair systems (Webb 1977). The net effect of these phenomena and their applicability to higher plant nucleic acid damage is not easily envisaged.

The primary site of UV damage to photosynthesis is in the reaction center of Photosystem II (Renger et al. this volume; Noorudeen and Kulandaivelu 1982) and most likely does not involve nucleic acids. For intact higher plants, interactions between UV-B and longer wavelength radiation have been frequently reported though the mechanisms are not understood. Plant leaves which have developed under low visible radiation conditions are considerably more sensitive to UV-B inhibition of photosynthesis (Teramura et al. 1980; Sisson and Caldwell 1976; Warner and Caldwell 1983). Yet, there is also some evidence that higher visible irradiance during UV-B irradiation increases the inhibition of photosynthesis even though the visible irradiation by itself is not sufficient to inhibit photosynthesis (Warner and Caldwell 1983). At present, one can only speculate about the mecha-

nisms involved in these interactions.

#### A Photosynthetic Inhibition Spectrum

Predicting the net effect of interactions between radiation of different wavelengths for phenomena such as nucleic acid damage or inhibition of photosynthesis is not possible at present even though the action spectra for some repair processes such as photoreactivation are known. Thus, in order to account for the synergistic effects of radiation at different wavelengths when "damage" action spectra are to be used as weighting functions for polychromatic radiation, one is forced to take a more empirical approach. This can be done by employing polychromatic radiation in the development of action spectra and using intact plant organs. In this process the biological responses to different combinations of polychromatic irradiation are determined and these responses and associated spectral irradiance data can be deconvoluted to yield an action spectrum (Rundel 1983). With respect to the ozone reduction problem, the most logical combinations of polychromatic irradiation involve a constant background of longwave UV-A and visible irradiance with increments of radiation at shorter wavelength intervals. This process can sacrifice some of the fine structure of an action spectrum, but this is of less concern for the purpose of weighting functions.

This series of polychromatic irradiation distributions should be planned to account for the tail of the action spectrum into the UV-A or visible waveband, as the case may be. Characteristics of the action spectrum below 280 nm are of no concern with respect to solar UV radiation changes because of the effectiveness of atmospheric ozone absorption, even in the case of a severely depleted ozone layer (Caldwell 1979). Yet, if a particular lamp system emits shorter wavelengths, the weighting function should include these as well.

To illustrate this polychromatic approach to action spectrum development, reduction of photosynthesis of an intact leaf of Rumex patientia will be depicted. Photosynthetic inhibition of higher plants by UV radiation is of potential concern with respect to ozone reduction. For some species under certain experimental conditions, solar UV radiation at flux rates now received at temperate latitudes has been shown to reduce photosynthesis (Bogenrieder and Klein 1977; Sisson and Caldwell 1977). Yet to be resolved, however, is the extent to which plants experience photosynthetic inhibition under field conditions, or how much they might be inhibited in the event of ozone layer reduction. Nevertheless, there is sufficient impetus to select net photosynthesis for action spectrum analysis because of its potential susceptibility to solar UV radiation and its obvious importance for plant biology. Furthermore, net photosynthesis is an integrated physiological process which requires the integrity of membrane systems and the coordinated action of photochemical and enzymatic processes. Thus, it also serves as a useful indicator of plant response to stress.

Methods: Assessment of photosynthetic depression resulting from UV irradiation involved the determination of net CO<sub>2</sub> uptake by plant leaves, exposure of the leaves to a particular polychromatic irradiation distribution, and then subsequent determination of CO<sub>2</sub> uptake capacity under identical conditions. Ideally, the leaves would be exposed to the inactivating UV irradiation over a period of several days or weeks as would occur under

field conditions. Unfortunately, this involves unreasonable biological and experimental complications. Leaf photosynthetic characteristics change appreciably with leaf age (e.g., Sestak 1977; Sisson and Caldwell 1977). These changes combined with the time and logistic requirements for such experiments render this approach infeasible. Thus, the irradiation periods ranged from one to 16 hours. Seven polychromatic radiation distributions were employed. For each, a dose-response relationship was developed. Even with these irradiation periods, such experiments are very time consuming.

The spectral irradiance for the seven polychromatic irradiation distributions are shown in Fig. 2. These were developed by using a 2.5-kW xenon high pressure lamp and a combination of dichroic and sharp cutoff filters. Much of the visible and infrared radiation was removed by the dichroic filter arrangement in order to prevent excessive leaf temperatures. Yet, there was sufficient visible flux ( $400 \mu\text{moles m}^{-2} \text{s}^{-1}$  between 400 and 700 nm) to drive photosynthesis of the plants during the UV irradiation. Leaves still intact with the remainder of the plant were placed on a slowly revolving stage in this radiation field to insure even irradiation of the leaves.

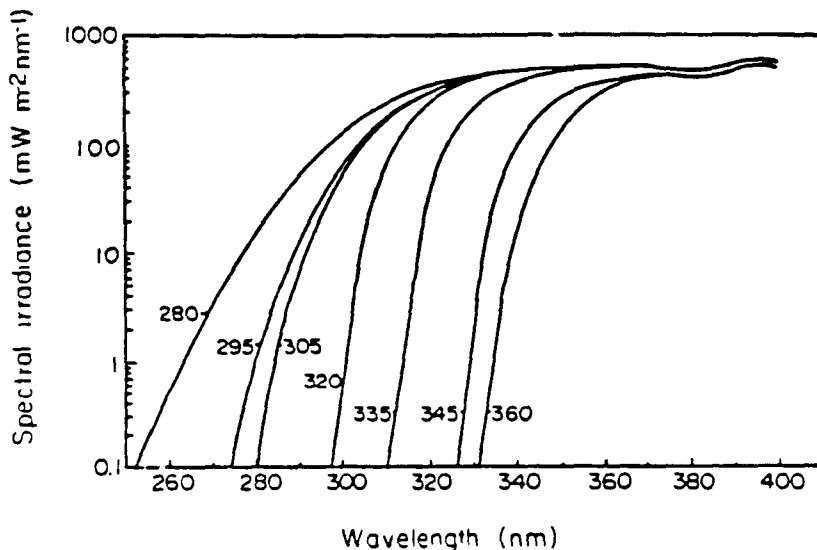


Fig. 2. Spectral irradiance for seven polychromatic irradiation distributions used in the development of an action spectrum for inhibition of photosynthesis. Radiation is supplied by a 2.5-kW xenon high pressure lamp and filtered with a combination of dichroic and absorption filters. The sharp cutoff filters used for each distribution are from the Schott WG series.

Net photosynthetic rates of intact leaves were assessed by measurements of net  $\text{CO}_2$  uptake under specific environmental conditions in a gas exchange cuvette. By measurement of simultaneous  $\text{CO}_2$  and water vapor flux of the foliage as well as other parameters including leaf temperature,  $\text{CO}_2$  concentration in the cuvette air, and water vapor concentration in the cuvette, it is possible to calculate intercellular  $\text{CO}_2$  concentrations within the leaf (e.g., Caldwell et al. 1977). Intercellular  $\text{CO}_2$  is influenced

primarily by photosynthetic rates,  $\text{CO}_2$  in the cuvette airstream, and diffusion resistance provided by stomata. Since photosynthesis is normally substrate limited, it is important to manage the cuvette conditions to maintain a constant intercellular  $\text{CO}_2$  concentration in the leaf before and after irradiation so that metabolic photosynthetic capacity of a leaf is assessed without the complication of changes in diffusion resistances between the leaf intercellular  $\text{CO}_2$  and the air. Direct coupling of the gas exchange system with a computer allows immediate assessment of these parameters so that adjustments in cuvette conditions can be made during the course of these measurements.

**Results and discussion:** The dose-response relationships for net photosynthetic inhibition of Rumex patientia leaves are shown in Fig. 3 for the different spectral irradiance distributions. Each data point represents a different leaf measured on a different date since each determination required a day to complete. Nevertheless, these dose-response data reveal linear relationships. The coefficients of determination,  $R^2$ , range between 0.63 and 0.98 with an average of 0.87. The spectral irradiance combination which included the least short wavelength radiation (WG 360, Fig. 2) did not result in inhibition of photosynthesis under these conditions even after 16 hours of exposure.

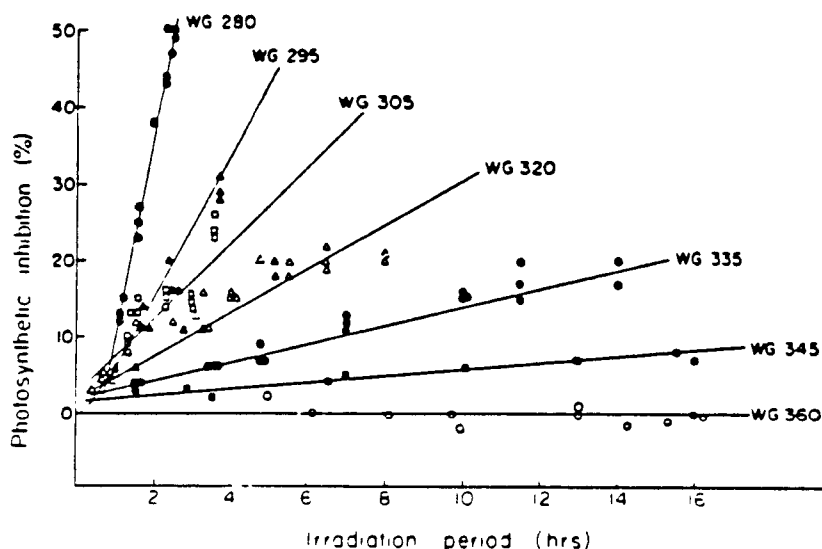


Fig. 3. Relative inhibition of net photosynthesis of intact Rumex patientia leaves exposed to the polychromatic irradiation combinations shown in Fig. 2.

These photosynthetic inhibition data indicate that when there was sensitivity to a particular irradiation distribution, we were dealing with a linear portion of the dose-response relationship. This is important in developing action spectra. If a particular dose-response relationship exhibits diminished slope as with saturation, these data cannot be compared with a dose-response relationship which is in the initial, linear phase. The dose-response relationships presented here indicate that it is suitable to utilize the slope of these linear regression relationships for biolog-

ical response in developing these action spectra.

When these slopes are taken as the relative effect for each spectral irradiance combination, an action spectrum can be deconvoluted from the slopes and respective spectral irradiance data (Rundel 1983). Several possible spectra can result depending on the exact procedure followed. The spectrum shown in Fig. 4 is the monotonic function that provided the best fit to the data (Rundel 1983).

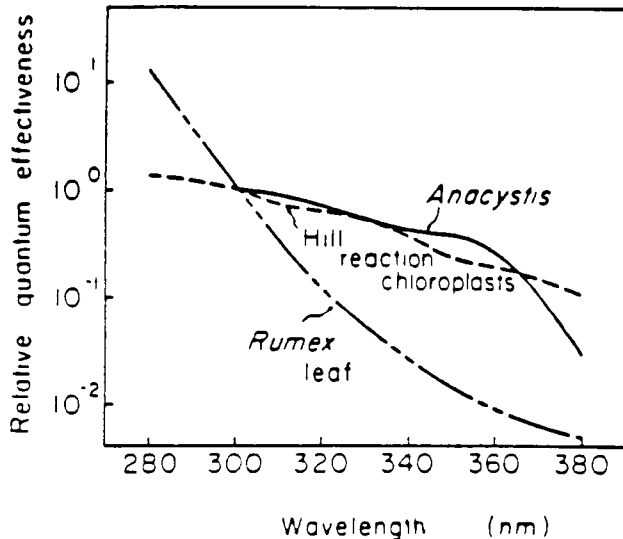


Fig. 4. Action spectrum for inhibition of photosynthesis for an intact leaf of Rumex patientia deconvoluted from the data of Figs. 2 and 3 by Rundel (1983) for his monotonic function that provided the best fit. Spectra for inhibition of Hill reaction in isolated spinach chloroplasts (Jones and Kok 1966) and of the Cyanobacterium, Anacystis, (Hirosawa and Miyachi 1983) are also shown. The two Hill reaction spectra were developed with monochromatic radiation.

The action spectrum deconvoluted from the polychromatic radiation study with intact leaves is considerably steeper than the spectrum for inhibition of a partial photosynthetic reaction, the Hill reaction, conducted by treating isolated spinach chloroplasts with monochromatic radiation (Jones and Kok 1966). The spectrum for inhibition of fluorescence rise time from spinach thylakoid suspensions (Rjörn et al. this volume) and a spectrum for Hill reaction inhibition of the Cyanobacterium, Anacystis nidulans, (Hirosawa and Miyachi 1983), also developed with monochromatic radiation, correspond closely with the spectrum of Jones and Kok. The two Hill reaction inhibition spectra are also shown in Fig. 4.

Preliminary results of more recent action spectrum studies for Rumex patientia and other species suggest that the action spectrum may exhibit steeper declines with increasing wavelength than the spectrum for Rumex shown in Fig. 4. This new work involves simultaneous UV irradiation and leaf gas exchange measurements. With a split-beam arrangement, the leaf is also simultaneously receiving high visible irradiation (800 to 1200  $\mu$ moles

$m^{-2} s^{-1}$ , depending on the species being investigated). Though the visible flux employed is still only 40 to 60 percent of that in midday solar radiation, photosynthesis is light saturated. Since subsequent action spectra conducted with higher visible irradiance may reveal steeper declines with increasing wavelength, the action spectrum shown in Fig. 4 for Rumex should be considered as only provisional. The importance of the rate of decline with increasing wavelength when action spectra are used as weighting functions is discussed in a subsequent section.

Although practical limitations do not permit these experiments to be performed with spectral irradiance that exactly matches that of solar radiation, this approach with polychromatic radiation and intact leaves should provide a much more realistic approximation of the ecologically relevant action spectra for photosynthetic inhibition. It also indicates that extrapolation from damage spectra of specific physiological reactions, as shown in Fig. 1, to intact organisms may not provide reliable results. As will be discussed in a subsequent section, there is also indirect evidence that the action spectrum developed for inhibition of photosynthesis by this polychromatic approach may be appropriate for plants in nature.

#### Action Spectra and Radiation Amplification Factors

One of the functions of action spectra in assessment of the ozone reduction problem is their use in evaluating radiation amplification factors, RAF, i.e., the relative increase in biologically effective UV radiation for a given level of ozone reduction. As noted in a previous section, all UV damage spectra exhibit a general decrease in effectiveness with increasing wavelength, though the rates of decline vary considerably (e.g., Fig. 1). Since solar spectral irradiance increases by orders of magnitude with increasing wavelength, the rate of decline of action spectra has a pronounced effect on the resulting RAF when these spectra are used as weighting functions. Furthermore, even though ozone reduction would only result in increases of solar spectral irradiance in the UV-B part of the spectrum (Caldwell 1981), the weighting function should include all wavelengths of the solar spectrum where the weighted spectral irradiance adds appreciably to the integral of Eq. (1). Although many UV-B biological damage spectra include the UV-A region, few extend far into the visible spectrum. This is not of great consequence if the effectiveness is already so low by 400 nm that the weighted visible flux would not contribute significantly to the total biologically effective flux (such as is the case for DNA damage), or if the action spectrum is already sufficiently flat so as to result in a negligible RAF (as is the case for the Hill reaction spectrum).

To illustrate the behavior of the RAF calculated with different action spectra, a variety of spectra currently in use, as well as the provisional photosynthetic inhibition action spectrum for Rumex, are portrayed in Fig. 5 and the respective RAF values for different total ozone column thickness relative to 0.32 cm in Fig. 6. The model of Green et al. (1980) was used to calculate the spectral irradiance. The action spectra have been chosen because they illustrate the RAF values for spectra with a broad range of slopes.

The DNA damage spectrum is a generalized spectrum compiled by Setlow (1974). The generalized plant damage spectrum is also the result of a

compilation of several plant damage spectra that exhibit similar characteristics (Caldwell 1971). The generalized plant damage spectrum terminates at 313.3 nm simply because that was the longest wavelength (an emission line from mercury vapor UV lamps) where information was available for these spectra at the time they were compiled. (If these spectra decline steeply beyond 313 nm as the DNA-damage spectrum does, the contribution of weighted spectral irradiance at wavelengths greater than 313 nm would be negligible for the total integrated biologically effective flux.) The Robertson-Berger, R-B, meter is a widely used integrating dosimeter for solar UV monitoring (Berger et al. 1975). The spectral response of this meter was originally designed to approximate that of human skin erythema. The provisional spectrum for photosynthetic inhibition of *Rumex* (Fig. 4) is also included; although preliminary data (cited previously) indicate that a steeper spectrum may be more appropriate and that this would result in greater RAF values.

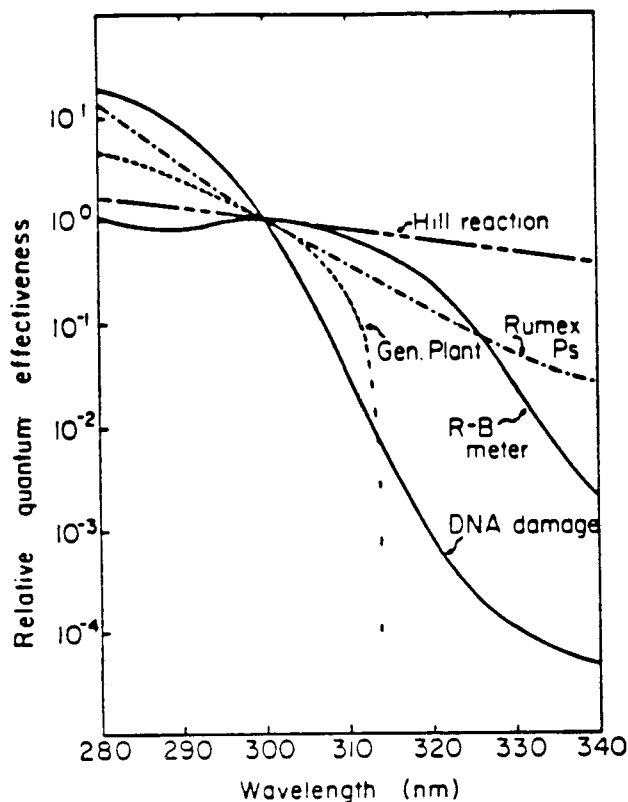


Fig. 5. Action spectra exhibiting different rates of decline with increasing wavelength. These include the spectrum for Hill reaction inhibition of spinach chloroplasts (Jones and Kok 1966), the *Rumex* leaf photosynthesis inhibition spectrum (Fig. 4), a spectrum for the Robertson-Berger meter (Robertson 1975), a generalized plant damage spectrum (Caldwell 1971) and a generalized DNA damage spectrum (Setlow 1974).

The RAF values in Fig. 6 are calculated over the waveband 290-380 nm. For the DNA and generalized plant damage spectra there would be no significant effect if the integral included longer wavelengths. For the Hill reaction and R-B meter spectra, the RAF values would be even smaller if longer wavelengths were included in the integration. The deconvoluted *Rumex* spectrum

is unreliable at longer wavelengths. As noted in the previous section, polychromatic irradiation which did not include wavelengths shorter than 330 nm had no effect on photosynthesis (Figs. 2 and 3). Also shown in Fig. 6 is a slope indicating a 2% increase of biologically damaging radiation for each 1% decrease of ozone column thickness which has commonly been used as a guideline for the RAF (National Academy of Sciences 1979).

Radiation amplification factors are dependent on the degree of ozone reduction and this dependency is more pronounced for steeper action spectra (Fig. 6). The RAF is also quite dependent on solar angle and, thus, RAF values appropriate for total daily effective radiation would be an integrated function for different times of day. The daily RAF would be dependent on latitude and time of year (National Academy of Sciences 1979). The RAF values in Fig. 6 are plotted for a solar angle from the zenith of  $33.6^\circ$  (air mass of 1.2). For the summer solstice at  $40^\circ$  latitude, these RAF values would also be approximately the same as total integrated daily dose RAF values.

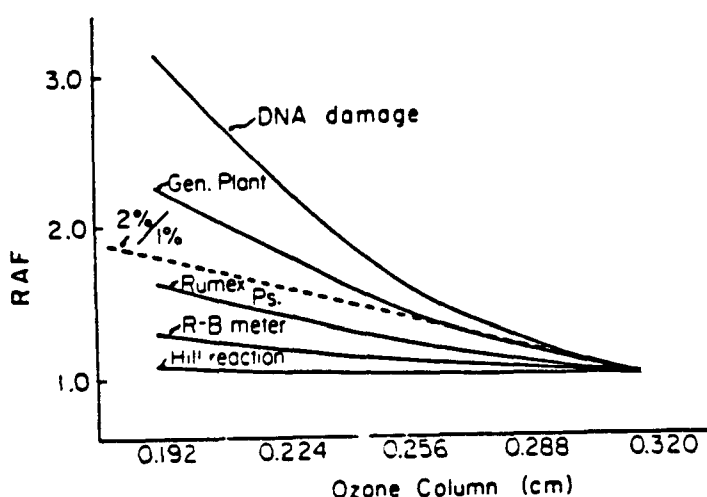


Fig. 6. Radiation amplification factors calculated for different ozone column thickness, relative to 0.32 cm, and a solar angle from the zenith of  $33.6^\circ$  calculated according to the action spectra shown in Fig. 5. The dashed line represents a case of 2% increase in biologically effective radiation for a 1% decrease of ozone. The model of Green et al. (1980) was used to calculate the solar spectral irradiance (direct beam + diffuse) used for those RAF values.

#### The Natural Latitudinal Gradient of Solar UV-B Radiation

Natural latitudinal gradients of solar UV-B radiation exist on the earth. This is primarily the result of differences in prevailing solar angles and total ozone column thickness at different latitudes (Caldwell 1981). Correlations between the latitudinal UV-B gradient and skin cancer incidence of selected human populations have been used as a tool to predict increases of skin cancer as a function of ozone reduction (e.g., National Academy of Sciences 1979). An analogous correlation between latitude and changes in crop yield or other nonhuman biological phenomena are too confounded with other environmental variables such as soils, temperature and moisture to be of use in predicting the consequences of ozone reduction. Nevertheless, controlled study of plant response to, and tolerance



of, UV-B irradiation by species from different latitudes can provide some useful insight as to how plants cope with different levels of UV-B irradiation. However, just as the magnitude of solar UV-B increase resulting from ozone reduction is dependent on the action spectrum used, the steepness of the present latitudinal gradient of solar UV-B irradiance is also quite dependent on the action spectrum used for evaluation.

The effective UV-B radiation for the season of year of maximum solar radiation at different latitudes is shown in Fig. 7. These are plotted relative to the radiation at 40° latitude. (The date of maximum solar radiation at each latitude corresponds to the time when solar zenith angles are minimal. Above 23° latitude this occurs at the summer solstice, but at latitudes less than 23°, this time is progressively closer to the equinoxes, about March 21 and September 23, which are the dates of maximum solar radiation at the equator.) Three different action spectra have been used as weighting functions to illustrate the dependence of this gradient on action spectrum characteristics. Just as the RAF is greater for steeper action spectra (Fig. 6), steeper action spectra also result in a more pronounced latitudinal gradient of solar UV-B irradiance.

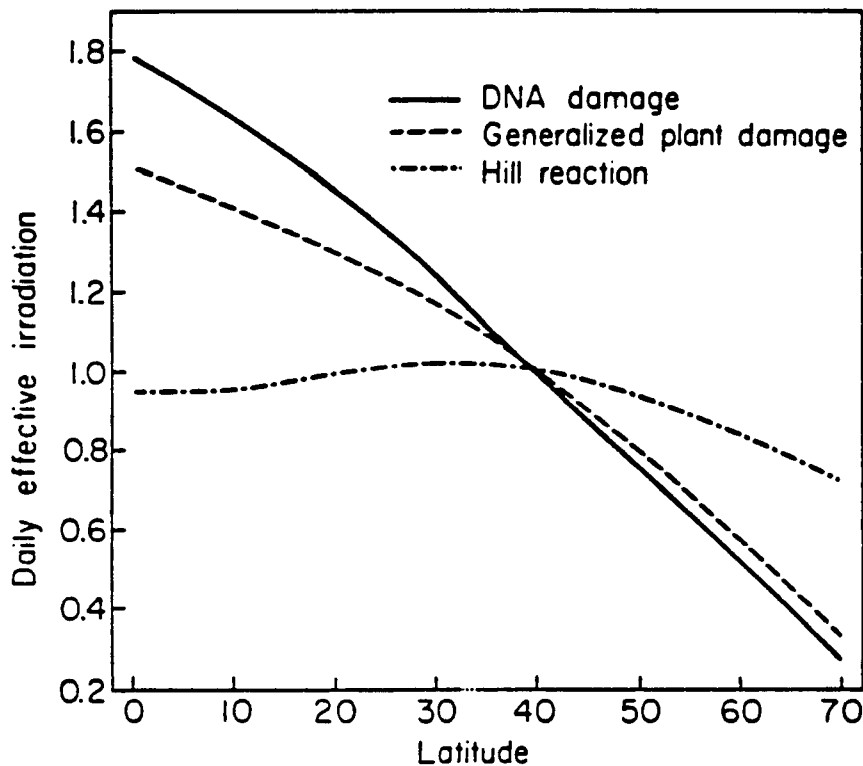


Fig. 7. Daily effective UV-B radiation for the season of year of maximum solar radiation at different latitudes relative to that at 40° latitude calculated according to the generalized DNA damage action spectrum (Setlow 1974), the generalized plant damage action spectrum (Caldwell 1971) and the Hill reaction inhibition spectrum (Jones and Kok, 1966).

If a spectrum has a rather slow rate of decline with increasing wavelength,

such as the Hill reaction spectrum, there is no latitudinal solar UV-B gradient. Thus, study of characteristics of plants that have originated from different latitudes can provide some indirect evidence of the type of UV damage action spectrum that is indeed appropriate for plants. For example, if a spectrum such as the Hill reaction is indeed representative of the spectrum for UV damage to plants, one might expect little correlation between the latitude of origin of plants and their sensitivity to UV-B radiation when this radiation is presented at sufficient flux densities to result in damage.

There are several lines of evidence that suggest that a sufficiently steep action spectrum for plant damage exists so that an appreciable latitudinal gradient of solar UV-B radiation has been extant. The first line of evidence is a correlation between the latitude of origin of crop species and their sensitivity to UV-B radiation as measured by a reduction of plant biomass in experiments with UV-B radiation lamps. Over 50% of the crop species which have originated from temperate latitudes were sensitive to UV-B radiation in these tests, whereas for crop species that have originated at low latitudes, only 20% were classified as sensitive (Teramura and Caldwell unpublished).

The second two lines of evidence are derived from a latitudinal gradient in the arctic-alpine life zone ranging from sea level locations in the Arctic to alpine elevations (3000-4000 m) at mid to low latitudes. In this situation an even steeper gradient should be expected because elevation above sea level is superimposed on the latitudinal gradient (Caldwell et al. 1980). A survey of UV optical properties of leaves from nonagricultural, as well as agricultural, plant species has been conducted by sampling plants in the field at various locations along this gradient and determining the UV epidermal transmittance of the leaves. Plants occurring in areas of high solar UV-B radiation, at low latitudes and high altitudes, exhibited a greater capacity to selectively absorb UV-B radiation in the upper tissue layers of the leaves (Robberecht et al. 1980). If the selective pressure for UV absorption in the epidermis of plant leaves were approximately the same at all locations along this gradient, such as would be the case if an action spectrum like that of the Hill reaction inhibition were appropriate for UV-B damage, one would not expect a correlation between latitude and UV-B filtration capacity of the leaf epidermis.

A third line of evidence involves the inherent differences in sensitivity of the photosynthetic system to UV-B radiation damage that have been demonstrated for species of the same genus or even races of the same species which occur in different locations on the latitudinal gradient of the arctic-alpine life zone (Caldwell et al. 1982). In these experiments, plants were cultured under identical conditions in environmental growth chambers before the sensitivity of their photosynthetic systems to the UV-B radiation was assessed. Arctic races or species consistently showed much greater sensitivity to UV-B radiation and this could not be solely attributed to differences in the optical properties of the leaf epidermis. Such evidence certainly supports the notion that a steeper action spectrum for photosynthetic damage by UV radiation such as that developed using polychromatic radiation (Fig. 4) would be more appropriate than an action spectrum such as that for the Hill reaction. Although all three lines of evidence are circumstantial, they support the notion that an appreciable RAF exists for higher plants.

## Biological Assessments and Errors Deriving from Action Spectra

Before radiation amplification factors can be used in assessment of biological and ecological consequences of ozone reduction, it is necessary to demonstrate biological effects of UV-B radiation. Ideally, one should establish a dose-response relationship. In any case, it is at least necessary to show a meaningful response at UV-B flux densities exceeding those currently in sunlight. (Investigations involving the removal of UV-B from solar radiation, such as with filters, have generally not resulted in significant plant responses (Caldwell 1968; Becwar et al. 1982; Caldwell 1981), although there are some notable exceptions (e.g., Bogenreider and Klein 1977).)

Experiments with lamps: One cannot easily simulate the solar spectral irradiance either with or without reduced ozone using UV lamps. Thus, weighted UV irradiance from the lamp system is compared with weighted solar UV irradiance as would occur with a particular solar angle, ozone concentration, etc. The most common lamps used are fluorescent lamps which emit principally in the UV-B region. The spectral irradiance from the most frequently used bulbs is shown in Fig. 8. As with all fluorescent lamps, these are basically low pressure mercury vapor lamps with a phosphor that fluoresces in a continuous spectrum -- in this case, mainly in the UV-B region, but some UV-C and UV-A radiation is included. Though most of the radiant emission from the bulbs comes from the fluorescing phosphor, the emission from the mercury vapor is also present and this appears as distinct lines in the spectrum. The fluorescent lamp manufactured by Philips Co. emits substantially more than the bulb of Westinghouse.

Filters are commonly employed to absorb the UV-C and short-wavelength UV-B radiation emitted by these bulbs. Investigators in Europe have commonly used the Philips bulbs with glass cutoff absorption filters (Schott WG series) for this purpose, while in North America, cellulose acetate plastic film has been used with the bulbs manufactured by Westinghouse (Caldwell et al. 1983). The glass absorption filters have the advantage of being stable in their transmittance, while the plastic film filters are considerably less expensive but exhibit decreased transmittance as they are exposed to UV radiation (Caldwell et al. 1983). The spectral irradiance from filtered and unfiltered lamps shown in Fig. 8 is provided as a comparison of these lamp and filter combinations. Naturally, individual lamps will vary in their emission and, as with all fluorescent lamps, their emission will decrease with age, especially during the first 100 hours of use, and with temperatures that are too warm or too cold for optimal operation (Rickford and Dunn 1972).

If filtered fluorescent lamps are the only source of UV radiation for plant experiments, the discrepancy between spectral irradiance received from the sun and that received from the lamps is considerable (Fig. 9a). When compared with the midday solar irradiance in the summer at temperate latitudes, a bank of filtered Westinghouse fluorescent lamps provide more shortwave UV-B radiation and more than an order of magnitude less longwave UV-B and UV-A radiation. Thus, the action spectrum used to weight the spectral irradiance for comparison of the lamp systems with solar radiation is particularly critical as will be demonstrated subsequently.

When such lamp systems are used to supplement the normal solar radiation, i.e., when plants are exposed both to the solar radiation as well as a

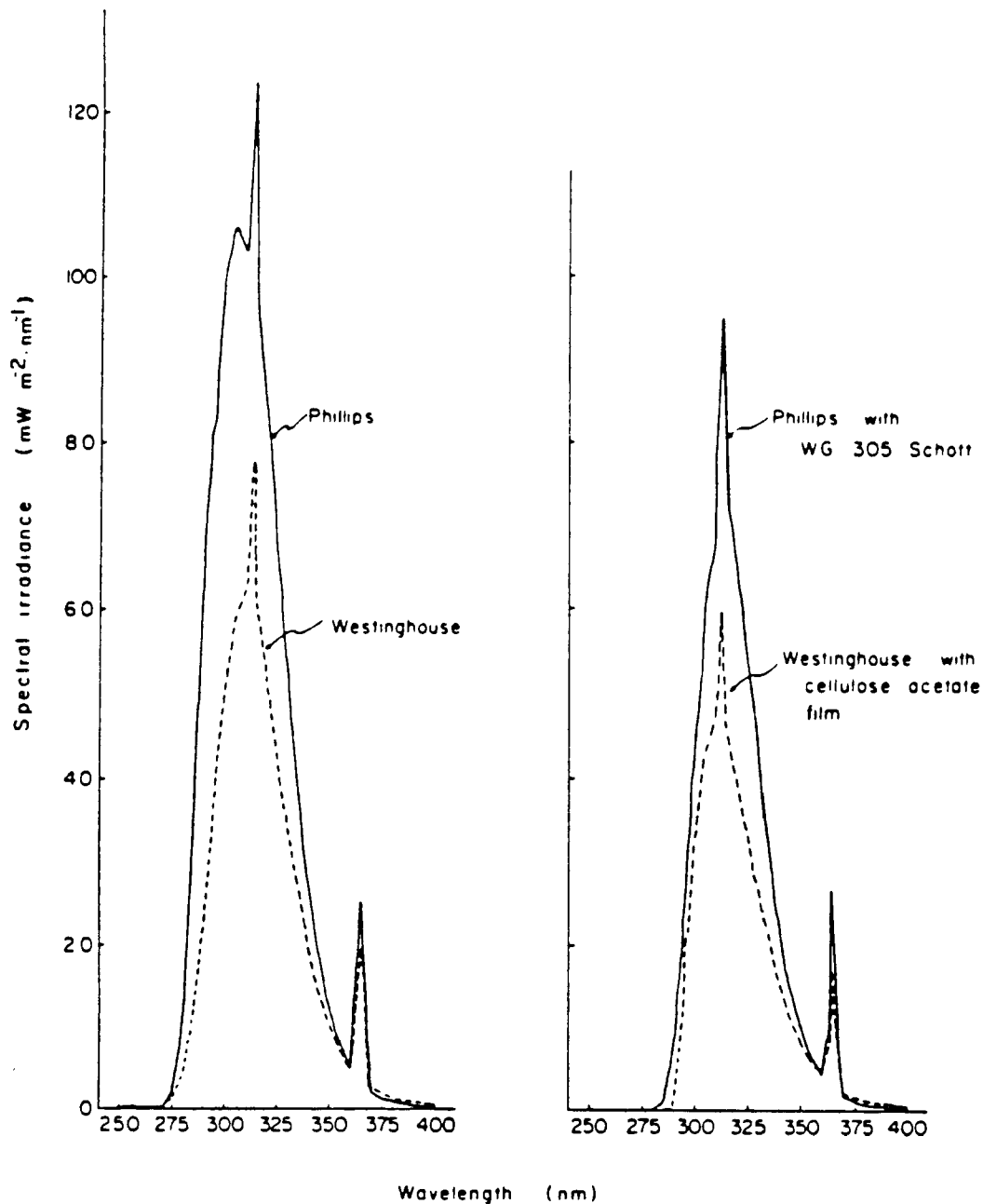


Fig. 8. The spectral irradiance at 30 cm from common fluorescent UV-B lamps with and without filters. The lamps and filters were new and the spectral irradiance was measured with a double monochromator spectroradiometer (Optronic Laboratories). The Philips TL 40W/12 and the Westinghouse FS40 lamps without filters are shown on the left and with filters on the right. Schott WG 305 sharp cutoff absorption filters (2 mm thickness) were used with the Philips lamp and cellulose acetate plastic film (0.13 mm thickness) with the Westinghouse lamp. These lamp/filter combinations have commonly been used in studies in Europe and North America, respectively.

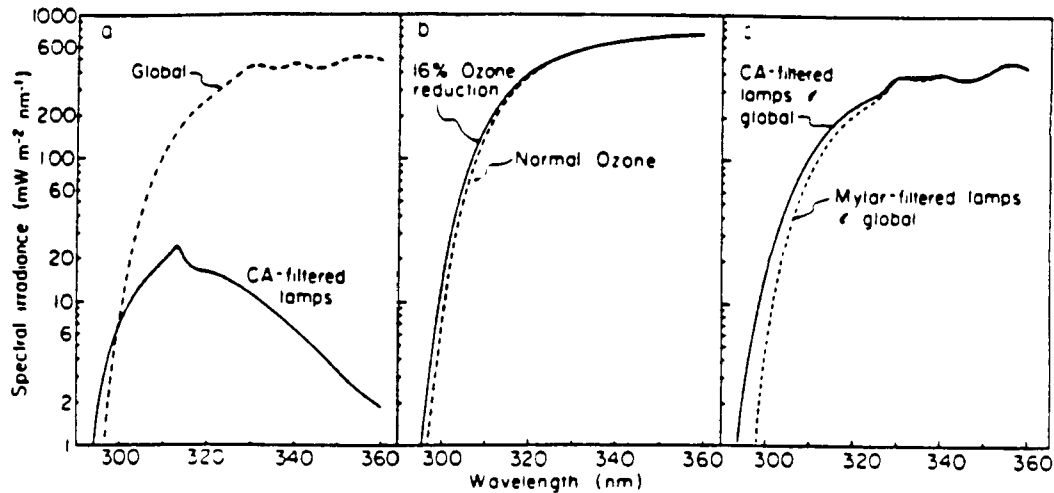


Fig. 9. Global (direct beam + diffuse) UV spectral irradiance and the spectral irradiance from filtered lamp systems used in experiments. In the left panel, a, global spectral irradiance as measured at solar noon on August 20 at 41° 45' N latitude and 1460 m elevation and the spectral irradiance from Westinghouse FS 40 lamps with cellulose acetate film filters (without background global radiation) are shown. The lamp system is adjusted to provide a UV-B supplement equivalent to a 16% ozone reduction under these conditions calculated according to the generalized plant damage action spectrum. In the middle panel, b, the theoretical global UV spectral irradiance for these conditions, as calculated by the model of Green et al. (1980), is shown for current ozone conditions as well as conditions with a 16% reduction of the atmospheric ozone layer. In the right panel, c, the UV spectral irradiance measured under lamp systems with cellulose acetate and Mylar film filters with the background global radiation is shown. The Mylar-filtered lamp system provides a control with the same UV-A irradiance and obstruction of global radiation as the CA-filtered lamps which constitute the enhancement treatment. The UV-A irradiance in both treatment and control is less than the ambient global shown in the left panel because of the obstruction created by the lamps. The UV-B supplement in the right panel represents the same effective UV-B radiation as that predicted with the Green et al. (1980) model when calculated using the generalized plant damage action spectrum. Adapted from Caldwell et al. (1983).

supplement from the filtered lamp bank, the discrepancy in spectral distribution is much less. Ideally, the supplemented UV spectral irradiance would only be that shown as the difference between solar spectral irradiance under normal conditions and with ozone reduction (Fig. 9b). Since the filtered fluorescent lamps emit longer wavelength radiation than is desired for the supplement, it is necessary to use control lamps which are identical except that they are filtered so as to exclude the UV-B radiation. Thus, the amount of UV-A radiation provided by the control lamps would be the same as that coming from the treatment lamps, and the other microenvironmental influences such as shading by the lamps would also

be the same. In Fig. 9c the resulting spectral irradiance under lamp banks with two different plastic film filters, corresponding to treatment and control, is shown with the solar radiation background. The difference between these is still not a perfect simulation of what would be calculated as the difference between solar spectral irradiance with and without ozone reduction; however, the correspondence is considerably better than when the lamps are used by themselves such as would be the case in a glasshouse, growth chamber or laboratory situation.

Error analysis: There are then two basic types of error that are involved in use of action spectra as weighting functions in biological assessments of ozone reduction, namely RAF errors and enhancement errors. The RAF errors are those resulting from an overestimation or underestimation of the radiation amplification factors by assuming an incorrect action spectrum. The RAF errors would be associated with application of dose-response relationships to the solar UV-B irradiance that would result from various scenarios of ozone reduction. For example, if a given amount of UV-B irradiation corresponding to 10% ozone reduction resulted in 5% reduction of photosynthesis, one would employ the RAF to extrapolate to other ozone reduction levels for a given latitude and season of year.

The enhancement error is that associated with relating UV-B radiation supplied by lamp systems in an experiment with solar UV-B radiation for a particular ozone level. For example, if one desires to provide a UV-B radiation supplement under field conditions corresponding to a 15% ozone reduction, and an incorrect action spectrum is used as a weighting factor for comparing UV irradiance from the lamps and the sun, an error in the desired enhancement will result. The enhancement error necessarily includes an RAF error -- namely that associated with calculating the effective UV irradiance corresponding to the 15% ozone reduction.

These two types of error are shown in Fig. 10 for a scenario in which the generalized plant damage action spectrum (Fig. 5) is employed for calculating the RAF and the effective UV radiation enhancement when the DNA-damage spectrum (Fig. 5) is indeed the most appropriate for plant damage. (This is, of course, hypothetical as the most appropriate action spectrum to represent higher plant damage is not known.) The discrepancy between RAF values calculated by the generalized plant damage and DNA damage spectra is illustrated in the upper portion of Fig. 10. With greater ozone reduction, which requires larger RAF values, the divergence from the diagonal 1:1 line increases, i.e., the difference between the RAF values calculated using the two action spectra increases. This is directly from information presented in Fig. 6. The differences in UV radiation enhancement in a field experiment that would result from use of the two action spectra are shown in the lower half of Fig. 10. In field experiments the lamps are used to supplement the solar radiation, and a certain amount of obstruction of the solar global (direct beam + diffuse) radiation inevitably results. The exact spectral distribution of the radiation reaching the plants in the enhancement experiments then depends on the mixture of global and lamp radiation. The relationship in Fig. 10 was determined from actual measurements of spectral irradiance under lamp systems in a field experiment. Each point represents a combination of the UV radiation from the lamps and the background global radiation convoluted using the two action spectra. Relative enhancement is the ratio of the UV-B radiation from the lamps plus the background global radiation to the ambient global radiation without the lamp systems for particular conditions. The range of values shown in

Fig. 10 results from different experiments in which enhancements corresponding with different levels of ozone reduction and different solar angles were used. The lamp system is specially modulated so that the amount of UV supplement is adjusted for particular solar conditions such as solar angle, atmospheric turbidity, current ozone concentrations, etc. (Caldwell et al. 1983). A linear regression fits these points adequately ( $r^2 = 0.96$ ). The discrepancy between relative enhancements calculated by the two action spectra is greater than the discrepancy between the RAF values calculated with the two spectra.

For the action spectra represented in this paper (Figs. 1, 4 and 5) and the filtered UV fluorescent lamps commonly used, (Fig. 8), the RAF and enhancement errors are in opposite directions as depicted in Fig. 11. These relative errors are shown as a function of ozone reduction for field enhancement experiments under temperate-latitude conditions in the summer as portrayed in Fig. 10. The scenario is the same, namely, that the generalized plant damage action spectrum was assumed while the DNA-damage spectrum is correct. Although the relative RAF errors are small for situations where the ozone reduction is small, this is not the case for the enhancement errors (Fig. 11).

If a different scenario is pursued such that the generalized plant damage spectrum is assumed, but a spectrum with a slower rate of decline with increasing wavelength, such as the R-B spectrum (Fig. 5), is correct, then the RAF and enhancement errors would be reversed -- an overestimation of the RAF and underestimation of the enhancement.

As shown in Fig. 9, field UV enhancement experiments provide a much closer simulation of the spectral irradiance resulting from ozone reduction than do experiments in glasshouses or growth chambers in which UV radiation is provided only by filtered fluorescent lamps, since there is no solar UV background. The enhancement errors that might result from use of an incorrect action spectrum for calculating the enhancement are considerably greater than for field experiments, as shown in Fig. 12. The spectral irradiance from filtered Philips and Westinghouse UV fluorescent tubes following aging of the lamps and filters for about 100 hours was used to calculate the errors shown in Fig. 12. The same spectral distribution is assumed for all enhancement levels in such experiments, which is normally the situation, as doses are typically adjusted by varying the number of lamps, distance between the lamps and the experimental objects, or use of neutral density filters. The errors portrayed here are striking, especially when one considers that the two action spectra used for this scenario are not so very dissimilar (Fig. 5). Other scenarios could easily lead to larger overestimation or underestimation errors for the calculated enhancement. Also, for the errors depicted in Fig. 12 the relative overestimation errors are greater at UV levels corresponding to smaller ozone reductions.

If a source of background UV radiation were present, such as from a xenon arc lamp, these errors could be substantially reduced. However, this would depend on the flux density and spectral distribution received from the background source. An empirical analysis of the errors for particular situations would need to be conducted. However, without knowledge of the most appropriate action spectra for plant damage, the error analysis remains as a heuristic exercise quite dependent on the action spectrum scenarios assumed.

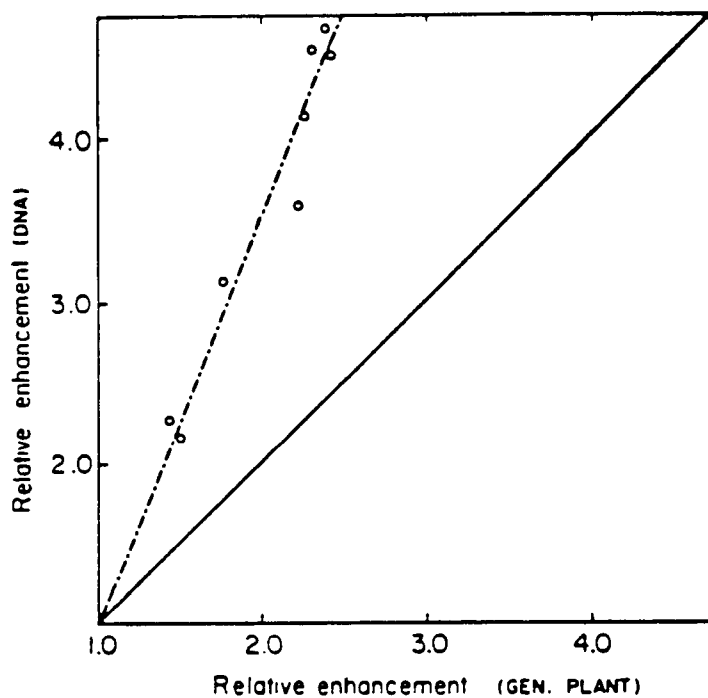
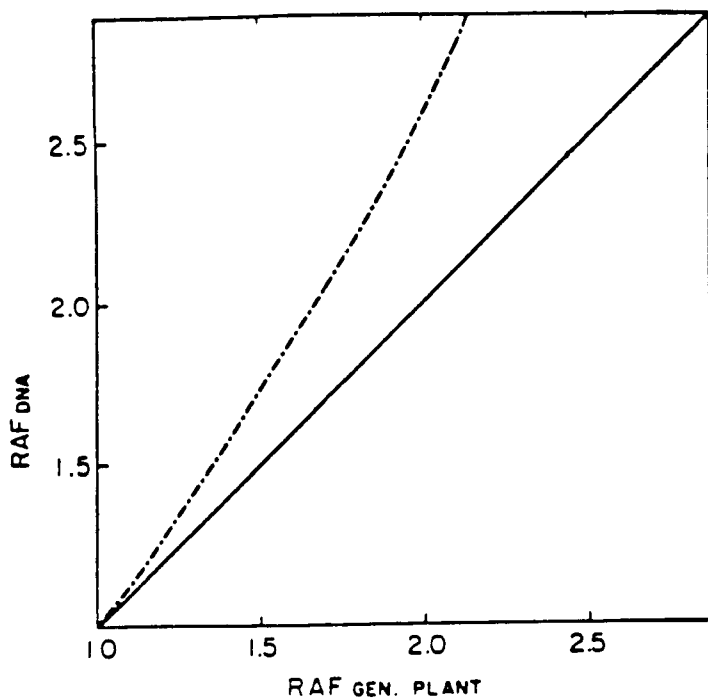


Fig. 10. The relationship between radiation amplification factors calculated with the generalized plant damage action spectrum and the generalized DNA damage action spectrum for different conditions and levels of ozone reduction (upper). The relative enhanced UV-B radiation in field experiments calculated according to the generalized plant damage spectrum and the generalized DNA damage spectrum for different conditions and levels of ozone reduction based on field spectral irradiance measurements (lower). The solid diagonal lines in both graphs represent a situation of equivalence for the RAF and relative enhancements calculated from the two spectra.



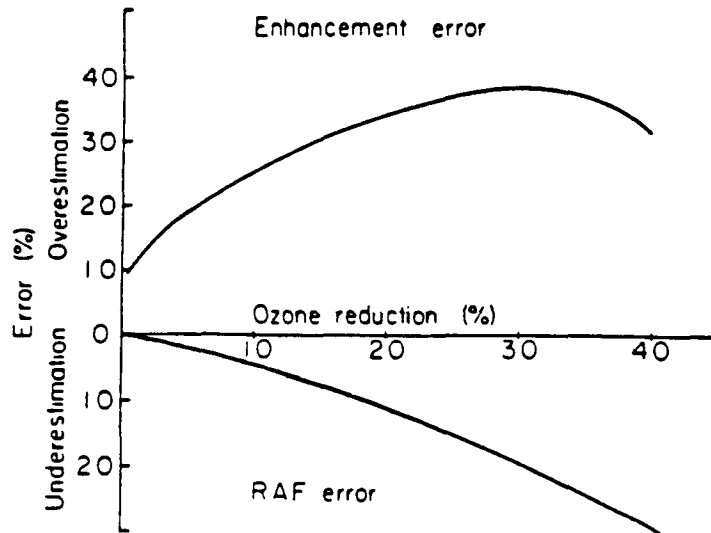


Fig. 11. Relative RAF and enhancement errors as a function of ozone reduction for field UV supplementation experiments under temperate-latitude conditions in the summer as portrayed in Fig. 10. The scenario for these errors is that the RAF values and the enhancements were calculated following the generalized plant action spectrum when the DNA damage spectrum was indeed correct.

#### CONCLUDING REMARKS

The potential errors resulting from assuming an incorrect action spectrum are compelling reasons for further action spectrum development. This should indeed be pursued. Yet, one should not expect that a single definitive action spectrum for higher plant damage will necessarily be forthcoming. It is unlikely when one considers the many basic modes of damage to plant tissues that UV radiation can effect (Fig. 1), the physiological and morphological diversity of plant species, and the interactions with other environmental factors, such as visible light, that can ensue.

Extrapolation from spectra of component reactions of isolated organelles to spectra of higher plant response in nature is precarious as shown for the case of photosynthetic damage (Fig. 4). Thus, use of intact plant organs and polychromatic radiation should be emphasized in further action spectrum development where these spectra bear on the ozone reduction problem. For damage to higher plant photosynthesis, the provisional action spectrum developed for *Rumex patientia* (Fig. 4) as well as circumstantial evidence from the natural latitudinal gradient indicate that the appropriate action spectrum is much steeper than the spectra for the Hill reaction. Thus, contrary to what one might conclude from component photosynthetic reactions, an appreciable RAF exists for damage to higher plant photosynthesis. More recent preliminary work with polychromatic radiation suggests that the spectrum may yet be even steeper and, therefore, one should view the *Rumex* spectrum presented here as only provisional.

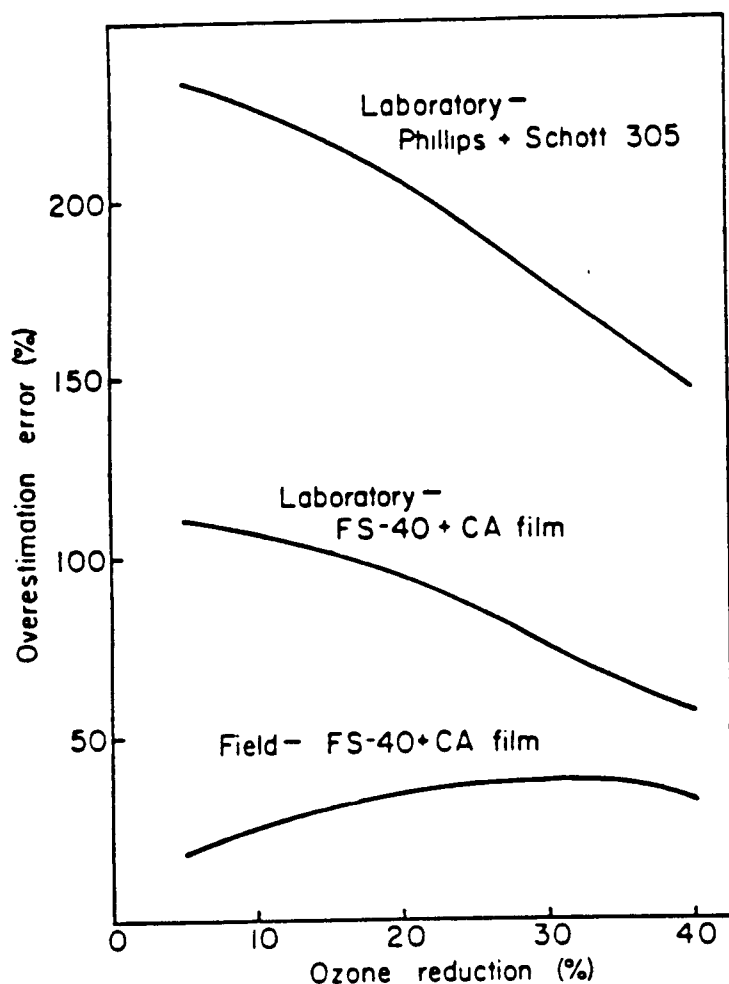


Fig. 12. Enhancement errors calculated according to the same scenario as for Fig. 11, but with enhancement experiments using different lamp systems. In the field supplementation experiment using Westinghouse FS40 lamps and cellulose acetate film, the errors are the same as portrayed in Fig. 11. Under laboratory conditions (which would correspond to glasshouse or growth chamber conditions with no background UV radiation) the Philips lamps with Schott WG 305 filters and the Westinghouse FS40 lamps with cellulose acetate film render the errors depicted. The lamps and filters were aged for about 100 hours for these measurements.

In our present state of ignorance concerning the most appropriate action spectra for higher plant damage, we feel it is reasonable to continue to use an action spectrum with an intermediate rate of decline with increasing wavelength, such as the generalized plant damage spectrum. An intermediate spectrum will, of course, yield intermediate RAF and enhancement values. If the appropriate spectra are later found to be either steeper or flatter, correction from an intermediate spectrum will be easier to conduct.

## ACKNOWLEDGMENTS

This work has been supported by the U.S. Environmental Protection Agency. Although the research described in this chapter has been funded primarily by the U.S. Environmental Protection Agency through Cooperative Agreement CR808670 to Utah State University, it has not been subjected to the Agency's required peer and policy review and therefore does not necessarily reflect the views of the Agency and no official endorsement should be inferred.

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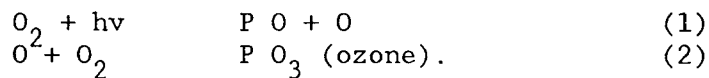
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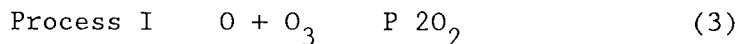
## APPENDIX B

## STRATOSPHERIC CHEMISTRY AND NATURE OF OZONE

Stratospheric ozone is the primary attenuator of extraterrestrial solar ultraviolet radiation and therefore determines the quality and quantity ultimately reaching the earth's surface. Approximately 95% of the total atmospheric ozone is found in the stratosphere, a region of the atmosphere about 16 to 50 km above the earth's surface at low latitudes and about 8 to 50 km at high latitudes. Global stratospheric ozone concentration is maintained by a balance of various processes that generate and remove it (Figure B-1). Ozone is formed by a reaction between atomic oxygen (O) with diatomic molecular oxygen (O<sub>2</sub>) and the process is initiated by the photolysis of diatomic oxygen:



The energy required for photolysis is 5.41 eV and is provided by solar radiation of wavelengths below 242 nm. According to figures published by the National Research Council (1982), photolysis provides a global source of ozone amounting to 50 billion metric tons per year, with more than 90% of this formed above 25 km. Approximately 1% of the ozone created in the stratosphere is removed by transport to the troposphere. The remainder is destroyed by chemical reactions involving oxygen (O), hydrogen (H), chlorine (Cl), and nitrogen (N) compounds, with the last three acting as catalysts in very low concentrations. The net effect of these various reactions is either the association of ozone with atomic oxygen to form O<sub>2</sub>, or the association of two ozone molecules:



The various reactions in process I are:



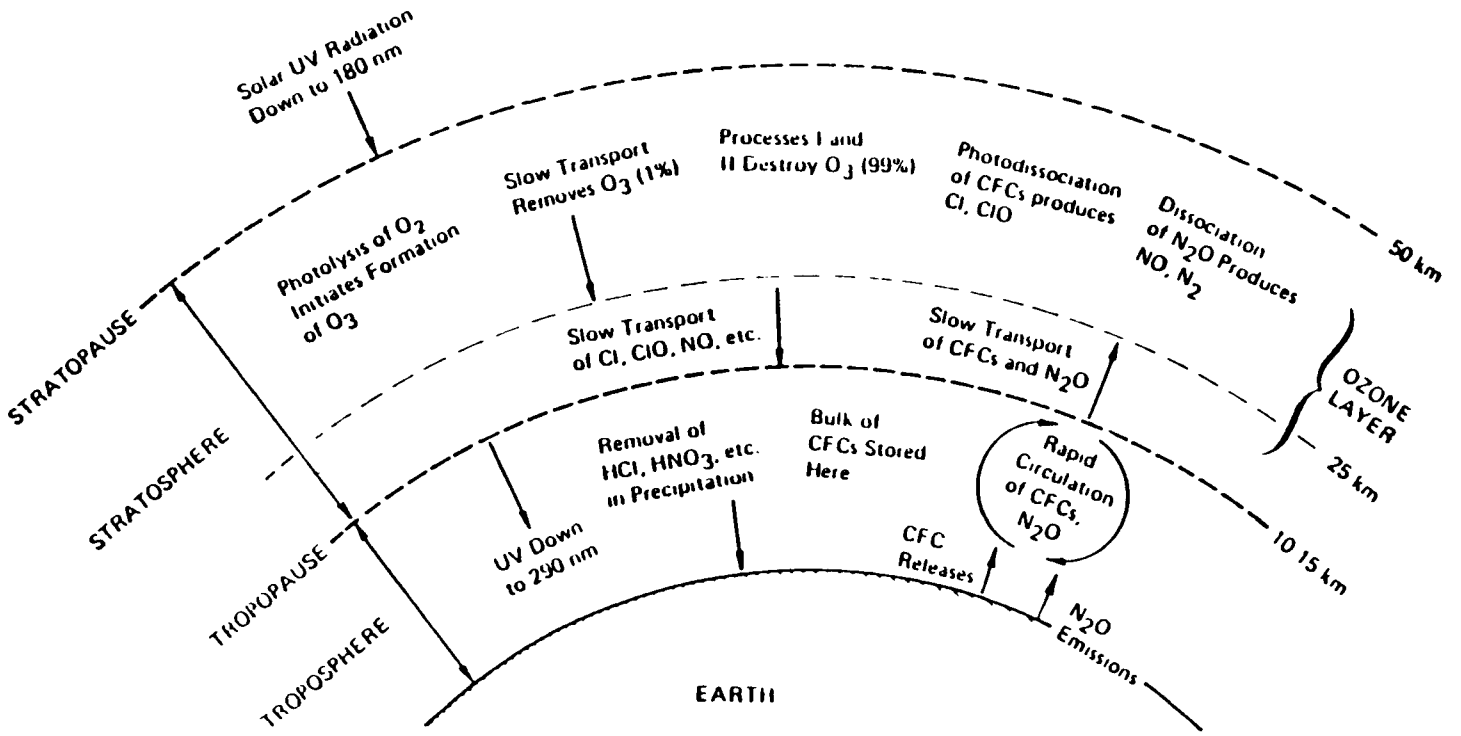
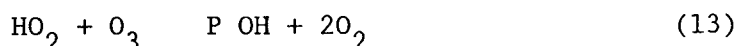
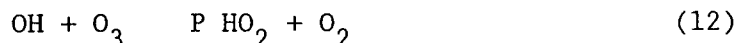


Fig. B-1. Representation of the processes that determine the concentration of ozone in the stratosphere (NRC 1982)

These reactions are limited by the availability of oxygen atoms, therefore effectively restricting them to altitudes above 25 km. The regeneration of oxygen occurs through photolysis of ozone:



The reaction schemes in process II where atomic oxygen is not limiting, are:



At altitudes between 25 and 45 km, reaction 7 accounts for approximately 45% of total ozone removal, while reactions 3 and 5 each account for about 20%, and reaction 9 for 10%. Below 25 km, reactions 12 and 13 account only for 1% (NRC 1982).

In reactions 5 and 7, Cl and NO are not consumed during ozone destruction because they are regenerated in reactions 6 and 8. A single chlorine atom can affect the recombination of  $10^4$  to  $10^5$  ozone molecules during its mean residence time in the stratosphere (about 2 years) before returning to the troposphere mainly as hydrochloric acid (HCl). The average NO<sub>x</sub> molecule is equally effective during its 2 years of residence in the stratosphere. Thus, the addition of these substances into the stratosphere profoundly affects the balance between production and removal process by which the total abundance of ozone is governed.

To date, approximately three parts per billion (ppb) of the lower stratosphere consists of Cl bound in organic molecules such as methyl chloride (CH<sub>3</sub>Cl), carbon tetrachloride (CCl<sub>4</sub>), and chlorofluorocarbons (CFC). Table B-1 lists the abundance of several prevalent species and their rate of release. Among these, methyl chloride is known to have substantial natural origins, while most others are anthropogenic. The global release of CFC-11 and CFC-12 from 1952 to 1980 is shown in Figure B-2. Although the release rate has decreased by about 20% from the peak rate of 1974, approximately 90% of all CFC-11 produced has been already released into the atmosphere and about 90% of this amount still remains in the atmosphere today (NAS 1984). The largest sources of CFCs are the industrial countries of the northern mid-latitudes, and the greatest concentrations are found over Europe and the eastern portions of the North America. The Atmospheric Lifetime Experiments (ALE) stations have been monitoring the concentration of CFC-11, CFC-12, CCl<sub>4</sub>, CH<sub>3</sub>CCl<sub>3</sub> and NO<sub>x</sub> in Ireland, Oregon (USA), Barbados, Samoa and Tasmania. Overall, there has been a steady increase in the concentrations of CFCs over the past decade. At altitudes above 20 km, halocarbons decompose in sunlight to release free chlorine. This free chlorine is converted to inorganic species including HCl, chlorine nitrate (ClNO<sub>2</sub>) and ClO. HCl is the major reservoir for chlorine at altitudes above 25 km.

The estimated ozone reduction due to changes in the rate of release of various chemicals is summarized in Table B-2. According to current theoretical estimates, continuing production of CFCs at rates of 3.1 million metric tons of CFC-11 and 4.3 million metric tons of CFC-12 annually (approximately the 1980 production rate) would lead to a steady-state



Table B-1. Concentration in the Lower Stratosphere and Release Rates of Major Sources of Chlorine in the Stratosphere (NRC 1982)

Compound	Concentration (ppb)		Rate of Release (million metric tons of Cl per year)
	Molecular	Chlorine	
Methyl chloride ( $\text{CH}_3\text{Cl}$ )	0.62	0.62	2 <sup>a</sup>
F-12 ( $\text{CF}_2\text{Cl}_2$ )	0.30	0.60	0.19 <sup>b</sup>
F-11 ( $\text{CFCl}_3$ )	0.18	0.54	0.20 <sup>b</sup>
Carbon tetrachloride ( $\text{CCl}_4$ )	0.13	0.52	0.053 <sup>c</sup>
Methyl chloroform ( $\text{CH}_3\text{CCl}_3$ )	0.11	0.33	0.35

<sup>a</sup> About 85 to 90 percent of  $\text{CH}_3\text{Cl}$  is naturally produced, the remainder being attributed to industrial sources. The total release rate varies slowly in time because of the large contributions of natural sources.

<sup>b</sup> 1980 release rate from "World Production and Release of Chlorofluorocarbons 11 and 12 through 1980," Chemical Manufacturers Association Fluorocarbon Program Panel, July 29, 1981. Release rate has decreased by about 20 percent from the peak rate of 1974.

<sup>c</sup> 1976 release rate. The release rate is apparently relatively constant, although somewhat uncertain.

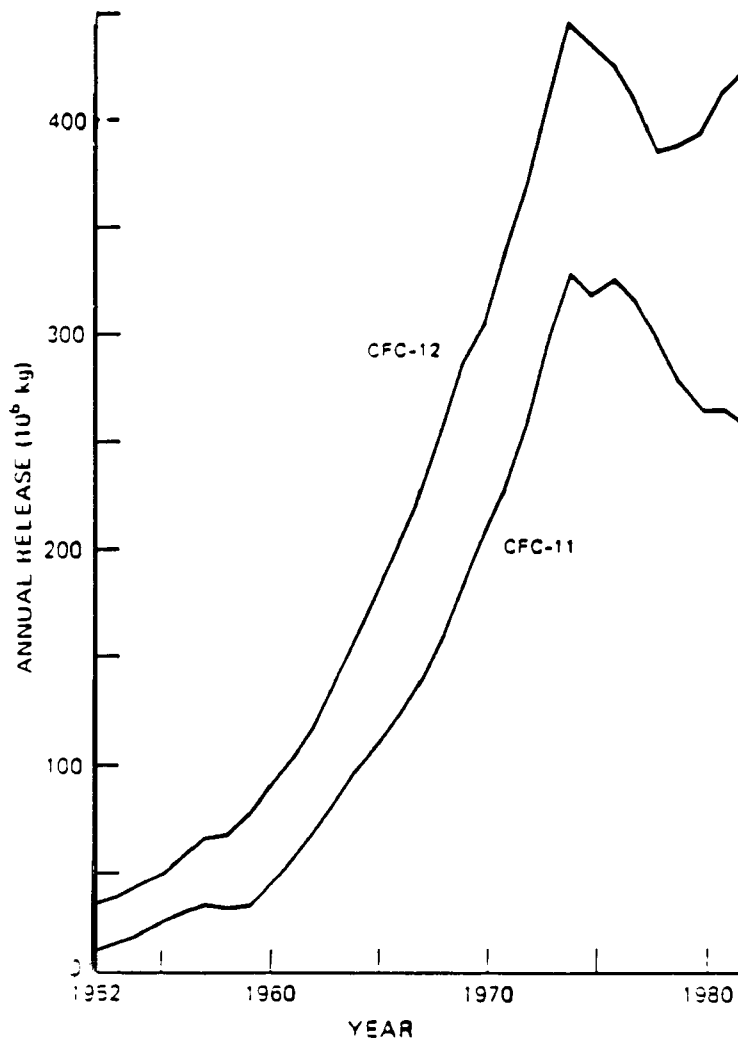


Fig. B-2. Estimated annual worldwide releases of CFC-11 and CFC-12, 1952-1980 NAS (1984).

Table B-2. Sensitivity of Total Column Ozone to Perturbing Influences  
(NAS 1984)

Trace Gas and Magnitude of Perturbation	Typical Estimate of Ozone Column Change (%)	Atmospheric Lifetime (years)	Principal Mode of Pollutant Removal
CFC-11 and -12 (1980 release rates)	-2 to -4	50-150	Photolysis of CFCs in middle stratosphere
Other halocarbons (2 ppbv $Cl_x$ increase)	-1	1-15	Decomposition of tropospheric chloro-carbon reservoir by reaction with OH
Subsonic aircraft ( $2 \times 10^9$ kg $NO_2$ /yr @ 12 km)	+1	1	Conversion to nitric acid and removal to surface
$N_2O$ (20% increase by 2050)	-4	100	Photolysis in stratosphere
$CH_4$ (doubling)	+3	10	Reaction with tropospheric OH
$CO_2$ (doubling)	+3 to +6	?	Uptake by oceans, sediment, and biosphere

\* Ozone column change (steady-state) was estimated using 1-D photochemical models.

reduction in the total column of ozone of 2-4% (NAS 1984). These calculations, however, were performed with a highly restrictive set of physical and chemical parameters and did not include temperature feedback. In the stratosphere, temperature increases with altitude due to the ozone absorbance of UV radiation. When temperature was included in the calculations, the reduction in the ozone column was computed to be 3-5%.

There have been many attempts over the past decade to estimate the magnitude of ozone change due to continuous CFC release. As seen in Figure B-3, there have been wide variations in the estimate of the magnitude of ozone reduction. Recently, there has been a trend toward lower calculated changes. In many ozone perturbation estimates, the release of CFCs is assumed to remain constant for 100 to 200 years, producing an eventual steady-state condition. However, this may not be true of future, long-term trends (as shown in Figure B-2) of worldwide release of CFCs. Wuebbles (NAS 1984) calculated a time-dependent ozone depletion for 18 halocarbon release scenarios (Figure B-4). In the scenarios projecting variations in CFC release rates by as much as 3% per year, the non steady-state total ozone reductions by the year 2030 ranged from 3% to 9%. With a 3% increase in CFC releases, however, the total ozone change falls precipitously beyond this date. These calculations demonstrate that the growth and decay of halocarbons occur over long time scales and that ozone depletion is very sensitive to growth in the rate of chlorine emissions.

A decade ago projections of large fleets of supersonic aircraft (SSTs) flying at altitudes of 20 km raised the concern over large-scale stratospheric ozone depletion due to the injection of nitrogen oxides (Johnston 1971). However, an economical SST system has not materialized and apparently will not be developed during this century. Nitrogen oxides are currently emitted into the lower stratosphere and upper troposphere (below 13 km) by subsonic commercial aircraft. At relatively low altitudes, photochemical reactions of  $\text{NO}_x$  in the presence of hydrocarbons generate small amounts of ozone (by an estimated 1%). However, large injections of  $\text{NO}_x$  at altitudes above 17 km could result in large reductions in stratospheric ozone. Global nitrous oxide concentrations appear to have increased by 2.7% over the past 16 years (from 292 ppb in 1964 to 300 ppb in 1980). It is likely to further increase with increases in emissions associated with agricultural activities, disposal of human and animal wastes, and possibly combustion (NAS 1984). The stratospheric decomposition of  $\text{N}_2\text{O}$  into  $\text{NO}_x$  occurs mainly in the middle stratosphere (between 20 and 40 km). In this region, catalytic ozone destruction by  $\text{NO}$  is extremely efficient and therefore increases in  $\text{N}_2\text{O}$  will result in decreases in stratosphere ozone. A 20% increase of  $\text{N}_2\text{O}$  by the year 2050 could decrease ozone concentrations by 4%. This could be expected if the currently observed rate of increase of  $\text{N}_2\text{O}$  concentrations were to continue over the next 100 years. However, it has been suggested that such reductions may be masked to some extent by increases in tropospheric ozone attributed to subsonic jets and urban smog (NAS 1984).

Methane ( $\text{CH}_4$ ) concentrations in the atmosphere are currently estimated to be increasing at a rate of 2% per year. Methane converts ozone-reactive chlorine atoms into  $\text{HCl}$ , which does not affect  $\text{O}_3$  directly. Hence, an increase in  $\text{CH}_4$  leads to a decrease in free chlorine, with a resultant reduction in ozone catalysis. Photodecomposed products of  $\text{CH}_4$  also interact

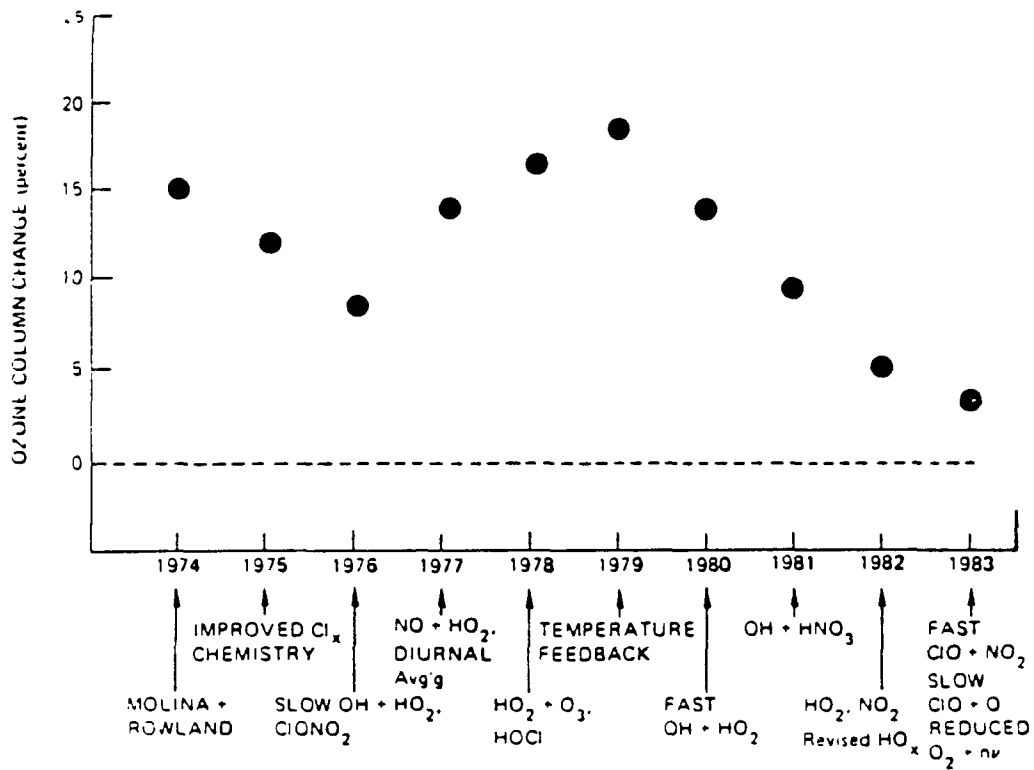


Fig. B-3. Estimates of steady-state reductions in total column ozone for continuous releases of CFCs at approximately 1975 rates as calculated from different chemical models. Changes in the models and simulation techniques are indicated in chronological order (adapted by NAS (1984) from Turco 1984).

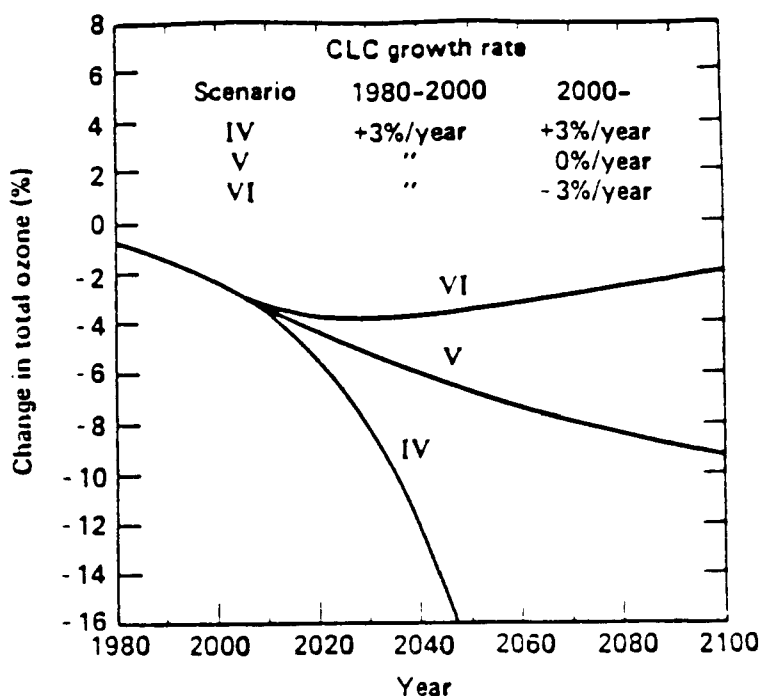


Fig. B-4. Time dependence of total column ozone calculated for several scenarios of CFC releases using 1982 chemistry. Calculations using more recent chemical models would yield smaller reductions in total ozone. (NAS, 1984)

with  $\text{NO}_x$  to produce ozone. If  $\text{CH}_4$  concentrations were to double those of current<sup>x</sup> values, the total ozone column could be increased by approximately 3% (NAS 1984).

Carbon dioxide ( $\text{CO}_2$ ) provides the dominant heat sink for the middle atmosphere through the emission of infrared radiation into space. Changes in  $\text{CO}_2$  concentration can alter the heat balance and temperature of the stratosphere and thereby the rates of basic chemical reactions. An increase in  $\text{CO}_2$  concentration lowers stratospheric temperatures and leads to increases in ozone concentrations. Current estimates of the net perturbations of stratospheric ozone resulting from a doubling of atmospheric  $\text{CO}_2$  are between 3% and 6% (NAS 1984).

It is evident from the above discussion that the effects of individual gases differ, some causing reductions in the total ozone column (CFCs, stratospheric  $\text{NO}_x$ ,  $\text{CH}_4$ ,  $\text{N}_2\text{O}$ ) and others leading to net increases (tropospheric  $\text{NO}_x$ ,  $\text{CH}_4$ ,  $\text{CO}_2$ ).<sup>x</sup> When the concentrations of these gases change simultaneously, the net effect on  $\text{O}_3$  may be quite complex. Few recent models have reported effects of the combined releases of several compounds on the stratospheric ozone concentration. Wuebbles (NAS 1984) estimated the time-course change in ozone corresponding to a combination of emissions. This scenario assumes that 1) release of CFCs,  $\text{CH}_3\text{CCl}_3$ , and  $\text{CCl}_4$  (designated CLC) is constant at 1980 levels; 2)  $\text{N}_2\text{O}$  increases at 0.2% per year; 3)  $\text{CO}_2$  increases at 0.6% per year; 4) aircraft emissions of  $\text{NO}_x$  below 13 km increase by a factor between 5 and 6 from 1975 to 1990 and remain<sup>x</sup> constant thereafter; and 5) there is a constant flux of  $\text{CH}_4$  at the earth's surface. According to this scenario, there will be a fraction<sup>x</sup> of a percent increase in the total column ozone by the year 2050. Atmospheric and Environmental Research (AER) and Du Pont (NAS 1984) have also calculated ozone depletion using scenarios for CLC,  $\text{CO}_2$ ,  $\text{N}_2\text{O}$  and  $\text{NO}_x$  similar to those used by Wuebbles, but with more recent chemistry and variable<sup>x</sup> fluxes of  $\text{CH}_4$  (AER 1.2; Du Pont 1.5%). If CFC releases are doubled by 1980, and  $\text{CH}_4$  release is constant, there would be 2% decrease in ozone concentration by the year 2050; if  $\text{CH}_4$  release increases, ozone concentration would increase by 4%.

Brasseur and Rudder (1984) have recently studied the sensitivity of the ozone layer to several chemical agents, individually and in coupled scenarios. The results are presented in Table B-3. The CFC perturbation (P) corresponds to a constant emission of  $\text{CFCl}_3$  ( $3.4 \times 10^5$  T/year),  $\text{CF}_2\text{Cl}_2$  ( $4.1 \times 10^5$  T/year),  $\text{CCl}_4$  ( $1.0 \times 10^5$  T/year), and  $\text{CH}_3\text{CCl}_3$  ( $3.6 \times 10^5$  T/year).<sup>2</sup> For other species ( $\text{CO}_2$ ,  $\text{N}_2\text{O}$  and  $\text{CH}_4$ ), current concentrations were doubled. They also considered temperature feedback in the model, and the simulations were made with presently adopted chemistry. The results show that the ozone depletion due to CFCs lies between 3% and 3.5%, whereas for  $\text{N}_2\text{O}$  it lies between 7.8% and 8.9%. A combination of different sources results in an ozone reduction of 1.3% to 6.8%. Compared to reports by NAS (1984), the computations made by Brasseur and Rudder (1984) indicate a larger influence of nitrogen-containing compounds and a smaller influence of CFCs. They attribute this difference to a smaller calculated value in OH radicals as a result of revisions in the reaction rates involved in the odd hydrogen destruction. This exemplifies the sensitivity of simulation models to revisions in reaction rates. These computations show that future ozone changes associated with CFCs may be drastically altered when other perturbing effects are included, and that the net ozone change may be extremely difficult to detect, since counteracting effects tend to reduce the perturbation signal in total ozone.

Table B-3. Perturbation of the Ozone Column (Brasseur and Rudder, 1984)

Case	CO <sub>2</sub>	N <sub>2</sub> O	CH <sub>4</sub>	CFCs	Temperature Feedback	% Change in Ozone
A				p*	Yes	-3.50
A'				p	No	-3.37
B	x 2				Yes	+3.14
C		x 2			Yes	-7.79
C'		x 2			No	-8.92
D			x 2		Yes	+0.97
D'			x 2		No	+0.87
E	x 2			P	Yes	-1.30
F		x 2	x 2	P	Yes	-5.56
F'		x 2	x 2	P	No	-6.84
G	x 2	x 2	x 2	P	Yes	-3.06

\* Emission of CFCs.



These models are severely limited because of the uncertain reliability of assumptions about release rates over many decades, photochemical processes and rate coefficients, and radiative-dynamical effects and interactions (NAS 1984). Schmailzl and Crutzen (1984) modelled the distribution of various ozone-destroying catalysts and the resulting ozone loss as a function of altitude, latitude, and season using recent photochemistry. They found a large imbalance in the ozone budget, with additional ozone destruction above 29 km and additional production below 29 km. They suggest this to be due to errors in reaction rate coefficients, in the source gas distribution, in the solar fluxes, and in other deficiencies in understanding stratospheric photochemistry. Until such inconsistencies are resolved, there will continue to be a high degree of uncertainty associated with our predictions of future changes in stratospheric ozone concentration.

APPENDIX C

**EFFECTS OF ULTRAVIOLET-B RADIATION ON  
THE GROWTH AND YIELD OF CROP PLANTS**

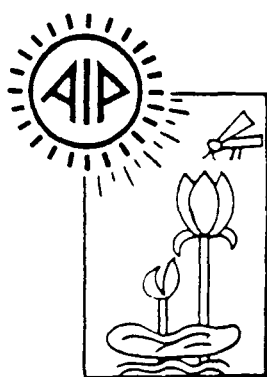
By

Alan H. Teramura

(from *Physiol Plant* 58:415-427, Copenhagen 1983)

## Effects of ultraviolet-B radiation on the growth and yield of crop plants

Alan H. Teramura



नृन जनाः सूर्येण प्रमृता

Teramura, A. H. 1983. Effects of ultraviolet-B radiation on the growth and yield of crop plants. - *Physiol. Plant.* 58: 415-427

This paper reviews growth chamber, greenhouse, and field studies on the effects of ultraviolet-B (UV-B, between 280 and 320 nm) radiation on agricultural crop plants. Our understanding of the physiological effects of UV-B radiation comes primarily from growth chamber studies, where UV-B is artificially supplied via filtered lamps. Both photosystems I and II, as well as carboxylating enzymes, are sensitive to UV-B radiation. Ultraviolet-B radiation also affects stomatal resistance, chlorophyll concentration, soluble leaf proteins, lipids, and carbohydrate pools. In general, the effects of UV-B radiation are accentuated by the low levels of visible radiation typically found inside growth chambers.

Ultraviolet-B radiation has also been shown to affect anatomical and morphological plant characteristics. Commonly observed UV-B induced changes include plant stunting, reductions in leaf area and total biomass, and alterations in the pattern of biomass partitioning into various plant organs. In sensitive plants, evidence of cell and tissue damage often appears on the upper leaf epidermis as bronzing, glazing, and chlorosis. Epidermal transmission in the UV region decreases in irradiated leaves. This decrease is primarily associated with a stimulation in flavonoid biosynthesis and is thought to be a protective, screening response to the deleterious effects of UV-B. A considerable degree of variability exists in sensitivity to UV-B radiation between different species. Approximately 30% of the species tested were resistant, another 20% were extremely sensitive, and the remainder were of intermediate sensitivity, in terms of reductions in total dry weight. In addition to this sizable interspecific variability, there appears to be a similarly wide intraspecific variability in UV-B response.

The effects of UV-B radiation on crop yield have only been examined in a limited number of field studies, with ambient levels of UV-B radiation being supplemented with fluorescent sun lamps. Due to various deficiencies, all these field experiments to date have only limited utility for assessing the potential impact of enhanced levels of UV-B on crop productivity.

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This paper is part of the contribution to the International Workshop on the Effects of Ultraviolet Radiation on Plants, held in Delhi, India, 1-5 November, 1982.

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Received 16 December, 1982; revised 15 March, 1983

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## Introduction

During the past decade, there has been considerable concern over reductions in stratospheric ozone concentration resulting from man's activities. Since stratospheric ozone is the primary attenuator of solar ultraviolet radiation, such a reduction would result in an increase in ultraviolet radiation reaching the earth's surface. Current estimates of ozone depletion during the next century range between 5 and 9% (National Academy of Sciences 1982). Atmospheric attenuation of solar radiation is wavelength dependent, therefore the anticipated spectral irradiation changes would occur within a relatively narrow waveband in the ultraviolet-B (UV-B) region (between 280–320 nm). Even under an unlikely 40% global ozone reduction (Green et al. 1974, 1980) radiation of shorter wavelengths (UV-C, 200–280 nm) would not penetrate the earth's atmosphere. Furthermore, since the ozone absorption coefficient is very low at longer wavelengths, UV-A radiation (320–400 nm) is also virtually unaffected by changes in stratospheric ozone concentration (Caldwell 1981). The intent of this article is specifically to review the effects of enhanced UV-B radiation on agricultural crops, as a result of ozone depletion.

For the purposes of this review, the term "crop" refers to an agricultural plant species that is either cultivated or domesticated for harvest. Putting this into perspective, there are over 350 000 species of plants in the world and over 80 000 of these are edible. Nevertheless, only about 3 000 are harvested by man and used for food (Miller 1982). Currently, only about 80 plant species have been domesticated (Ehrlich et al. 1977), and of these only 15 species supply nearly all the food calories and three-fourths of the protein to the world (Tab. 1). Three members of the Poaceae, rice, wheat and corn supply two-thirds of these calories and one-half of the protein.

A summary of the effects of UV-B radiation on the physiology and growth of crops is presented in Tab. 2. A brief description of these effects and generalities drawn from specific studies follows below.

*Abbreviations* – UV-A, ultraviolet radiation between 320 and 400 nm; UV-B, ultraviolet radiation between 280 and 320 nm; UV-C, ultraviolet radiation between 200 and 280 nm; PAR, photosynthetically active radiation between 400 and 700 nm;

Tab. 1 Major world food crops and production (Food and Agriculture Organization 1981)

Crop	Production (10 <sup>6</sup> metric tons)	Crop	Production
<i>Cereals</i>		<i>Sugar crops</i>	
rice	413	sugar cane	775
wheat	458	sugar beet	281
corn	451	<i>Root crops</i>	
sorghum	72	sweet potato	146
barley	158	cassava	127
<i>Legumes (pulses)</i>		<i>Tree crops</i>	
soybean	88	coconut	37
peanut	19	banana	40
bean	42	nuts	4

PS I, photosystem I; PS II, photosystem II; C<sub>3</sub>, plants with ribulose-bisphosphate carboxylase-oxygenase as primary carboxylating enzyme; C<sub>4</sub>, plants with phosphoenol-pyruvate carboxylase as primary carboxylating enzyme; RuBPCase, ribulose-1,5-bisphosphate carboxylase-oxygenase; R, red radiation; FR, far-red radiation; SLW, specific leaf weight

## Physiological and biochemical effects of UV-B radiation

Ultraviolet radiation can affect the carbon balance of crops in at least 4 different ways by affecting: 1) the primary photochemical events and electron transport reactions, 2) the dark reactions fixing carbon into reduced compounds, 3) dark respiration, and 4) stomatal resistance.

### Photosynthetic processes

Although there are large species differences in sensitivity, UV-B radiation generally results in reductions in net photosynthesis. These reductions are paralleled by decreases in Hill activity in crops such as pea (*Pisum sativum* L.; Brandle et al. 1977, Garrard et al. 1976, Van et al. 1977), collard (*Brassica oleraceae* L. cv. acephala; Van et al. 1977, Basiouny et al. 1978), and soybean (*Glycine max* (L.) Merr; Basiouny et al. 1978, Vu et al. 1981), indicating the sensitivity of photosystem II (PS II) to UV-B radiation. Both Brandle et al. (1977) and Van et al. (1977) concluded that although cyclic photophosphorylation (PS I) was also somewhat sensitive to UV-B radiation, the primary effect involved PS II. In a study of the effects of UV-B radiation on several C<sub>3</sub> and C<sub>4</sub> crops, Basiouny et al. (1978) found that C<sub>3</sub> species were generally more sensitive than those with the C<sub>4</sub> photosynthetic pathway. This sensitivity among other factors, was associated with significant reductions in Hill activity. However, in peanut (*Arachis hypogaea* L.), a "resistant" C<sub>3</sub> species, Hill activity was

Tab 2 A summary of the effects of UV-B radiation on crop growth.

	References*
<b>A Physiological/biochemical effects</b>	
1 Photosynthesis	1, 4, 5, 7, 10, 11, 12, 18, 32, 37, 38, 40, 41, 43, 44, 45, 47, 48, 49, 55
Hill reaction	1, 5, 12, 20, 38, 41, 44, 49
Electron transport	12, 44
RuBP carboxylase	1, 20, 38, 44, 46, 47, 48
PEP carboxylase	47
Dark respiration	12, 18, 37, 40
Stomata	7, 12, 37, 39, 40
Photosynthetic pigments	1, 5, 16, 18, 20, 38, 40, 41, 42, 46, 48, 49, 55, 56, 57
2 Soluble proteins	1, 5, 16, 18, 20, 38, 40, 41, 42, 46, 47, 48, 49, 57, 58
3 Lipids	18, 41, 42, 57
4 Carbohydrates	2, 18, 20
5 Non-photosynthetic pigments	3, 7, 15, 16, 30, 31, 32, 38, 41, 42, 51, 52, 53, 54, 55, 56, 57, 58
6 Plant hormones	15, 51, 52, 53
7 Ion transport	3, 6
<b>B Morphological/anatomical effects</b>	
1 Leaf area	3, 5, 8, 9, 16, 32, 36, 37, 38, 39, 41, 42, 48, 50, 57, 58
2 Specific leaf weight	8, 9, 37, 48
3 Epidermal transmission	6, 19, 30, 31, 55
4 Bronzing/glazing/chlorosis	1, 3, 6, 7, 8, 9, 21, 30, 39, 40, 41, 42, 46, 47, 48, 49, 50, 56
5 Seedling growth/stunting	3, 5, 8, 9, 21, 32, 36, 37, 38, 39, 41, 42, 46, 49, 50, 51, 54, 56, 57
6 Dry matter production/allocation	5, 6, 8, 9, 14, 16, 18, 21, 22, 36, 37, 41, 42, 43, 45, 49, 50, 56, 57
7 Yield	2, 4, 8, 18, 22
<b>C Response differences</b>	
1 Interspecific (species differences)	1, 2, 4, 5, 6, 7, 8, 10, 14, 16, 18, 20, 21, 22, 30, 36, 39, 41, 42, 43, 44, 45, 46, 47, 50, 51, 54, 55, 56, 57, 58
2 Intraspecific (cultivar differences)	3, 7, 8, 9, 16, 50
<b>D Environmental interactions</b>	
1 Visible radiation (photoprotection)	7, 35, 36, 40, 45
2 Water stress	37, 39, 58

\* 1. Allen et al. 1978; 2. Ambler et al. 1978; 3. Ambler et al. 1975; 4. Bartholic et al. 1975; 5. Basiouny et al. 1978; 6. Benedict 1934; 7. Bennett 1981; 8. Biggs and Kossuth 1978; 9. Biggs et al. 1981; 10. Bogenrieder 1982; 11. Bogenrieder and Klein 1978; 12. Brandle et al. 1977; 14. Caldwell et al. 1975; 15. Drumm-Herrel and Mohr 1981; 16. Dumpert and Boscher 1982; 18. Esser 1980; 19. Gausman et al. 1975; 20. Garrard et al. 1976; 21. Krizek 1975; 22. Hart et al. 1975; 30. Robberecht and Caldwell 1978; 31. Robberecht et al. 1980; 32. Sisson 1981; 35. Teramura 1982; 36. Teramura 1980; 37. Teramura and Perry 1982; 38. Teramura and Caldwell 1981; 39. Teramura et al. 1983; 40. Teramura et al. 1980; 41. Tevini and Iwanzik 1982; 42. Tevini et al. 1981; 43. Van et al. 1975; 44. Van et al. 1977; 45. Van et al. 1976; 46. Vu et al. 1983; 47. Vu et al. 1982a; 48. Vu et al. 1982b; 49. Vu et al. 1981; 50. Vu et al. 1978; 51. Wellmann 1982; 52. Wellmann 1975; 53. Wellmann 1971; 54. Chassagne et al. 1981a; 55. Chassagne et al. 1981b; 56. Hashimoto and Tajima 1980; 57. Tevini et al. 1982; 58. Tevini et al. 1983.

unaffected by UV-B radiation. Similarly, Hill activity was unaffected in all the resistant  $C_4$  species.

Reductions in net photosynthesis were also coincident with ultrastructural damage to chloroplasts in pea (Brandle et al. 1977) and soybean (Allen et al. 1978). Disruption of the membrane structural integrity partially damages components necessary for both light and dark reactions of photosynthesis. High UV-B irradiance also significantly increases mesophyll (residual) resistance to carbon dioxide and thereby limits net photosynthesis in a number of plant species (Brandle et al.

1977, Sisson and Caldwell 1976, Teramura et al. 1980, Teramura and Perry 1982). This resistance term includes resistance associated with both electron transport and carboxylation reactions in photosynthesis (Jarvis 1971, Nobel 1974).

Tevini et al. (1981) reported large increases in soluble leaf proteins in barley (*Hordeum vulgare* L.), corn (*Zea mays* L.), bean (*Phaseolus vulgaris* L.) and radish (*Raphanus sativus* L.) grown and exposed to a high UV-B radiation dose. The authors indicated this might be a reflection of increased synthesis of aromatic amino

acids, the precursors for flavonoid biosynthesis. In an outdoor field experiment, Esser (1980) also found that soluble leaf proteins in potato (*Solanum tuberosum* L.), radish, bean, and spinach (*Spinacia oleracea* L.) increased with increasing UV-B irradiance. However, for plants grown under low levels of visible radiation, UV-B radiation has also been shown to be effective in decreasing total soluble leaf proteins in sensitive crops (Basiouny et al. 1978, Vu et al. 1982a, b). Due to the disparate nature of these studies, these contrasting findings may be the result of differences in experimental conditions, the UV-B irradiance employed, or the reflection of species response differences to UV-B radiation. Vu et al. (1982a) found that total soluble leaf proteins on a fresh weight basis increased after UV-B irradiation in tomato (*Lycopersicon esculentum* Mill.) and corn, but was reduced in soybean and pea. Additionally there is evidence that UV-B radiation increases soluble leaf proteins only during early leaf development in soybean, and decreases thereafter (Vu et al. 1982b).

Since as much as 50% of the total soluble leaf proteins may be in the form of the major  $C_3$  carboxylating enzyme, RuBPCase (Steinback 1981), a reduction in leaf protein may be a reflection of a decrease in carboxylating enzyme concentration. Increasing UV-B radiation produced reductions in RuBPCase activity in 4-week-old soybean and pea, and in 8-week-old tomato in shaded ( $0.22-0.25 \text{ mmol m}^{-2} \text{ s}^{-1}$ ) photosynthetically active radiation, PAR) greenhouse experiments (Vu et al. 1982a, b). Although net photosynthesis in pea and cabbage (*Brassica oleracea* L. cv. capitata) had been shown to be sensitive to UV-B radiation (Van et al. 1976), Garrard et al. (1976) found no significant differences in RuBPCase activity in these same crops. This apparent discrepancy may be the result of differences in UV-B irradiance or due to different growth conditions. It is now well documented for a number of plant species that net photosynthesis is more sensitive to UV-B radiation when plants are grown under low levels of visible radiation (Sisson and Caldwell 1976, Teramura et al. 1980, Teramura 1982). Recently Vu et al. (1983) examined the effects of UV-B radiation on RuBPCase concentration and activity in greenhouse-grown pea and soybean. They found that high UV-B irradiance, corresponding to a 36% decrease in stratospheric ozone concentration, reduced RuBPCase activity by as much as 40–60% of Mylar control levels, and that this reduction was due to a decrease in the amount of carboxylating enzyme present, and not due to enzyme inactivation.

#### Dark respiration

The carbon balance of crops can also be affected by changes in dark respiration. After only 5 h of UV-B irradiation, dark respiration was significantly greater in pea exposed to a moderate UV-B irradiance (Brandle et al. 1977). Sisson and Caldwell (1976) found that dark respiration was increased after only 2 days of moderate

UV-B radiation in *Rumex patientia* L., a very UV-B sensitive herbaceous plant. In soybean, however, Teramura et al. (1980) found that dark respiration was unaffected by low UV-B irradiance under a range of different PAR growth conditions. With the paucity of information available, it cannot be concluded that dark respiration in sensitive species is generally affected by UV-B radiation. Furthermore, no conclusive data exist on the effects of UV-B radiation on photorespiration in crop plants, other than some preliminary studies by Esser (1980).

#### Stomata

Net photosynthesis can also be limited by the diffusion of carbon dioxide entering the leaf through the stomata. Although net photosynthesis was significantly reduced after 4 h of UV-B irradiation in pea, stomatal resistance was unaffected (Brandle et al. 1977). Stomatal resistance, accounting for 10–20% of the total leaf resistance to carbon dioxide in soybean, was increased after a 2-week exposure to relatively low UV-B irradiance (Teramura et al. 1980). Bennett (1981), using high UV-B irradiance in greenhouses and growth chambers, found small increases in stomatal resistance for bean, soybean, and cucumber (*Cucumis sativus* L.), which coincided with significant reductions in net photosynthesis. He also found that adaxial stomatal resistance in one bean cultivar was somewhat more sensitive to UV-B radiation than abaxial stomata. In a growth chamber study on cucumber and radish, Teramura et al. (1983) found that moderate levels of UV-B radiation produced only small increases in stomatal resistance in radish after 12 days exposure, but had dramatic effects on cucumber. After only 1 day of irradiation, adaxial stomatal resistance in cucumber increased by 3-fold and remained high for 8 or 9 days, and then dramatically decreased. By this time, cucumber had apparently lost stomatal function as evidenced from diurnal studies on stomatal response to water stress.

#### Photosynthetic pigments

The photostability of chlorophylls has also received considerable attention. Basiouny et al. (1978) found that reductions in total dry weight and net photosynthesis were paralleled by reductions in total chlorophyll concentration in collard, oats (*Avena sativa* L.), and soybean ( $C_3$  species sensitive to UV-B radiation). Meanwhile, chlorophyll concentration in resistant  $C_3$  and  $C_4$  species was unaffected. They found no selective differences in the chlorophyll *a* or *b* concentration of sensitive plants. High UV-B irradiance in combination with low PAR growth levels produced significant reductions in chlorophyll concentration in bean and cabbage (Garrard et al. 1976), pea (Vu et al. 1983), soybean (Vu et al. 1983, 1982, 1981), bean, barley, and corn (Tevini et al. 1981). In general, these studies indicated that the degree of chlorophyll destruction was a

function of UV-B irradiance, and that although less affected, carotenoids responded similarly. The effects of UV-B radiation on chlorophyll *a/b* ratios differed somewhat between studies and therefore could reflect species differences. Vu et al. (1981) reported that chlorophyll *a/b* ratios decreased with increasing UV-B irradiance in soybean, but increased in pea at high UV irradiance (Vu et al. 1983). Tevini et al. (1981) concluded that high UV-B irradiance inhibited the biosynthesis of chlorophyll *b* more than *a*, since *a/b* ratios increased in bean, barley, radish, and corn. In contrast, when soybean was grown under a range of PAR growth regimes in combination with low and moderate UV-B irradiance, there appeared to be no effect on total chlorophyll concentration, despite large effects on net photosynthesis (Teramura et al. 1980). In fact, when soybean leaves were expanded under  $0.75 \text{ mmol m}^{-2} \text{ s}^{-1}$  PAR and moderate UV-B irradiance, there was an apparent stimulation in chlorophyll biosynthesis (Teramura and Caldwell 1981). In a field experiment, Esser (1980) found that chlorophyll concentration decreased in bean and increased in spinach under high UV-B irradiance while potato, barley and radish were unaffected. The reason for a reduction in chlorophyll and carotenoid concentrations after UV-B irradiation is still unclear. It could be the result of an inhibition of chlorophyll biosynthesis, or due to the degradation of these pigments or their precursors. Due to the large differences both in growth and treatment conditions, more studies are necessary to determine whether these differential responses are species specific or artifacts of the experiments themselves.

#### Lipids and carbohydrates

A combination of low PAR and high, continuous UV-B irradiance produced large reductions in the total lipid content of corn and bean seedlings after only 5 to 10 days. Higher irradiance also reduced lipid concentrations in barley (Tevini et al. 1981). It appears from this study that UV-B radiation has a differential effect on various membrane systems. The galactolipids, which are principally found in chloroplasts, were greatly reduced in barley, corn, bean, and radish seedlings. This was also paralleled by large decreases in chlorophyll concentration in these crops. Shifts in specific galactolipid concentration were noted to be similar to the pattern found during tissue senescence. Changes in the phospholipids, which occur in generally all membranes, were seen in bean and corn, but not in barley or radish. Under field conditions, Esser (1980) found that total lipids increased in bean and cabbage, decreased in spinach, and were unaffected in potato grown under unfiltered UV lamps. Due to the unnatural conditions under which the plants were grown and irradiated, however, further interpretation of these two studies must be made with caution. Further work is needed to substantiate these observations.

In growth chamber studies, Garrard et al. (1976) found that high UV-B irradiance produced substantial reductions in the major carbohydrate components of tomato, cabbage, and collard while it had little effect on peanut and corn. UV-B radiation quantitatively affected reducing sugars, sucrose, starch, and non-structural carbohydrates. Of the five crops tested, tomato was the most adversely affected in each case. In a field study using unfiltered lamps, Ambler et al. (1978) found that massive UV enhancements resulted in a 17–20% increase in sugar beet (*Beta vulgaris* L.) root sucrose, despite reductions in shoot dry weight and root fresh weight. In another field experiment, low supplemental UV-B irradiance was supplied by sunlamps filtered with Schott WG 305 cut-off filters, and high irradiance (UV-B and UV-C) was supplied by unfiltered lamps (Esser 1980). Under these conditions, reducing sugars and starch were only reduced under the unfiltered lamps in spinach and radish, while bean showed slight increases in these carbohydrate pools. Once more, these studies indicate that UV-B radiation is most effective when PAR is low during growth.

#### Non-photosynthetic pigments

The attenuation of UV-B radiation by outer leaf tissue layers is one means of reducing the UV-B flux received at potentially sensitive sites. This may represent an adaptive response to UV-B radiation. In a survey of epidermal transmission of nearly 70 native plants (Gausman et al. 1975, Robberecht and Caldwell 1978, Robberecht et al. 1980), it was found that epidermal transmission in the UV-B waveband was generally below 10%. Furthermore, epidermal transmission was lowest for plants growing in regions of high, naturally occurring UV-B flux, and increased as UV-B radiation diminished along a latitudinal gradient. Much of this UV-B attenuation was removed upon methanolic extraction of the epidermis, suggesting that phenolic compounds such as flavonoids were important in the absorption of UV-B radiation. Such compounds produce ideal UV screens since they are nearly transparent in the visible region, while possessing high absorption coefficients in the UV region. In greenhouse experiments, epidermal transmission was significantly reduced by UV-B radiation in corn (Robberecht and Caldwell 1978) and pea (Robberecht et al. 1980).

Under low PAR growth regimes and high UV-B irradiance, Tevini et al. (1981) found that a high concentration of flavonoids (water extractable) was produced by seedlings which appeared to be relatively resistant to UV-B radiation (barley and radish). In contrast, very little flavonoid production was found in the sensitive species, corn and bean. Flavonoid content in barley leaves rose in direct response to increasing UV-B irradiance, suggesting that this might be a protective response. Nevertheless, moderate UV-B irradiance produced significant reductions in net photosynthesis

despite an increase in flavonoid concentration (methanolic extractable) throughout leaf ontogeny in soybean (Teramura and Caldwell 1981). Similarly, Sisson (1981) found that leaf expansion and net photosynthesis in squash (*Cucurbita pepo* L.) were repressed by moderate UV-B irradiance, although flavonoid absorbance (methanolic extractable) substantially increased. Flavonoid concentration (acetone extractable) also greatly increased in pea (Vu et al. 1983) and soybean (Vu et al. 1981) leaves grown under high UV-B irradiance. UV-B radiation has also been shown to stimulate flavonoid biosynthesis in parsley (*Petroselinum hortense* Hoffm.) cell suspension cultures (Wellmann 1971, 1975), and this induction apparently involves the phytochrome system. Flavone glucoside synthesis was stimulated by a 1 h pre-irradiation with UV-B and this was further enhanced by a subsequent 15 h FR irradiation. This FR effect was reversed by R irradiation; however, neither R nor FR had any effect without pre-irradiation with UV-B. Wellmann (1982) has also recently reported that flavonoid formation is stimulated by UV-B irradiation in parsley and dill (*Anethum graveolens* L.) hypocotyl and roots, and of wheat (*Triticum aestivum* L.) and rye coleoptiles. Due to its rapid and dose dependent response, its high quantum effectiveness near 290 nm, and the strong UV-B absorption it appears that flavonoid biosynthesis in these systems is a protective reaction against UV-B radiation.

High UV-B irradiance has been reported to increase anthocyanin production in several crop species. Ambler et al. (1975) and Bennett (1981) have reported the formation of a red pigment, presumably anthocyanins, in cotton (*Gossypium hirsutum* L.) petioles. Recently, Drumm-Herrel and Mohr (1981) demonstrated that anthocyanin synthesis in sorghum (*Sorghum vulgare* Pers.) mesocotyls involved interactions between UV-A, UV-B, and phytochrome photoreceptors. UV-B induced anthocyanin production has also been reported in mustard hypocotyls, and corn, wheat, and rye (*Secale cereale* L.) coleoptiles (Wellmann 1982). Although this pigment production represents a specific UV-B effect, anthocyanin biosynthesis may not be particularly adaptive since it has little absorption in the UV-B waveband.

#### **Ion transport**

Very little work has been done on the effects of UV-B radiation on ion transport. In an early study, Benedict (1934) concluded that UV-B radiation between 290 and 310 nm stimulated growth and increased calcium content in tomato, soybean, and cucumber. Radiation below 265 nm was inhibitory. However, these data must be viewed with caution due to the extremely low visible light growth conditions (approximately  $0.04 \text{ mmol m}^{-2} \text{ s}^{-1}$  PAR) used in this study. More recently, Ambler et al. (1975) examined the influence of UV-B radiation on  $^{65}\text{Zn}$  translocation in seedlings of two cotton cultivars.

In general,  $^{65}\text{Zn}$  translocation from cotyledons into shoots was proportionately reduced as UV-B irradiance increased.

### **Morphological and anatomical effects of UV-B radiation**

#### **Leaf area and specific leaf weight**

Among the most sensitive plant organs to environmental stress are plant leaves. Leaf area is generally reduced by temperature, water, mineral, or salt stresses. Therefore, it is not surprising that leaf area is also reduced by UV-B radiation. In an extensive growth chamber study screening over 70 unrelated crop species and cultivars, Biggs and Kossuth (1978) found that leaf area was significantly reduced in over 60% of the cases. The most sensitive crops included soybean, bean, pea, cowpea [*Vigna unguiculata* (L.) Walp.], cucumber, watermelon (*Citrullus vulgaris* L.) rhubarb (*Rheum raphanocum* L.), rutabaga [*Brassica napobrassica* (L.) Mill.], kohlrabi (*Brassica oleracea* L. cv. gongyloides), and brussels sprouts (*B. oleracea* L. cv. gemmifera), while little effect was noted in rice (*Oryza sativa* L.), wheat, barley, millet (*Pennisetum glaucum* L.), oats, peanut, cotton, and sunflower (*Helianthus annuus* L.). In the most sensitive plants, leaf expansion was reduced by 60–70% (Tevini et al. 1981, Biggs et al. 1981). It must be noted, however, that such large area reductions are only found in studies utilizing very low PAR. Teramura (1980) found that UV-B radiation was more efficient at reducing leaf expansion in soybean under decreasing PAR. Growth in moderate UV-B irradiance and high PAR had no significant effect on soybean leaf area, and in fact, ambient UV-B irradiance may even stimulate leaf expansion (Teramura and Caldwell 1981). In field grown crops, leaf expansion was substantially increased by moderate UV-B radiation enhancements in potato (70% increase) and mustard (30% increase), while leaf expansion was unaffected in corn, cowpea, peanut, rice, and radish (Biggs and Kossuth 1978). It is noteworthy that cowpea and mustard were among the most sensitive crops in terms of leaf area reduction based on growth chamber data, while field experiments indicated they were among those most resistant. This suggests that qualitative as well as quantitative differences exist between plants grown in growth chambers and those grown in the field. Nevertheless, a few very sensitive species such as squash (*Cucurbita pepo* L.; Sisson 1981) and cucumber (Teramura et al. 1983) do show significant leaf area reductions even when irradiated with moderate levels of UV-B and high PAR, indicating their potential sensitivity under natural conditions.

Plants may also adapt to a UV-B radiation environment by increasing their specific leaf weight (SLW), the ratio of leaf mass to area. In this manner, upper leaf tissue layers might act as anatomical screens or filters to decrease UV-B transmission into sensitive underlying



areas. Specific leaf weight was found to increase in a number of soybean cultivars exposed to UV-B radiation (Biggs et al. 1981, Vu et al. 1982). However, in a screening experiment of 82 different crop and other economically important species conducted in growth chambers (Biggs and Kossuth 1978), SLW changes did not always correspond with UV-B radiation resistance, as was anticipated. In fact, SLW was unaffected by UV-B radiation in many plants and decreased in response to UV-B radiation in some species. Therefore, this anatomical manifestation alone is insufficient to protect crops from UV-B radiation and cannot be used as an indicator characteristic of UV-B radiation stress *per se*.

#### **Bronzing, glazing and chlorosis**

UV-B radiation also produces bronzing, scorching, glazing or chlorosis in leaves of susceptible plants such as soybean (Vu et al. 1983, Biggs et al. 1981), pea (Vu et al. 1978) and cucumber (Teramura et al. 1983). Under high UV-B irradiance, even relatively resistant crops such as barley (Tevini et al. 1981) and cotton (Ambler et al. 1975, Krizek 1975) show these effects. However, these symptoms are nearly always associated with plants grown under either high UV-B irradiance or with moderate UV-B irradiance but low PAR. In field studies with high UV irradiance supplied by unfiltered lamps, these symptoms have not been reported. Nevertheless, a few crops such as cucumber and at least one cultivar of soybean (cv. Hardee) do seem to develop some of these manifestations when grown under moderate UV-B irradiance and high PAR (Teramura et al. 1980, Teramura et al. 1983), indicating that they may occur in natural conditions. Robberecht and Caldwell (1978) reported that leaf bronzing was not apparent in corn, but did develop in tomato exposed to UV-B radiation in a greenhouse. The authors suggested that this might be partially due to differences in UV-B epidermal transmittance, since a significant increase in flavonoid biosynthesis was found in corn, but not in tomato. The presence and effectiveness of UV-B absorbing pigments in the leaf epidermis may be implicated in explaining some of the differences in observed leaf symptoms discussed above.

#### **Plant stunting**

One of the most common observations on seedling growth after UV-B irradiation is stunting or dwarfing, primarily resulting from a decrease in internode length. Similar to bronzing and chlorosis, stunting is exacerbated by high UV-B irradiation and low PAR. In a greenhouse study, Teramura (1980) found that after 6 or 7 weeks exposure to a range of moderate UV-B irradiance, stunting in wheat and soybean was only observed in plants grown under shaded conditions. In fact, under unshaded conditions more closely ap-

proximating those of the field (average mid-day PAR =  $1.6 \text{ mmol m}^{-2} \text{ s}^{-1}$ ), soybean which did not receive any UV-B radiation were shorter than those grown under low and moderate levels of UV-B. Stunting in soybean was primarily due to shorter internodes and not a reduction in node number. This suggested that UV-B radiation did not simply delay the rate of plant development, but rather involved some intrinsic growth characteristics. In a field experiment, Biggs and Kossuth (1978) reported that the height of the main stalk in corn was reduced by UV-B radiation, although their data indicate that the greatest reduction occurred under the lowest UV-B radiation enhancement. In the same study, rice height was unaffected and squash even showed a slight stimulation of growth. In another field experiment, Ambler et al. (1978) found that high UV (UV-B and UV-C) irradiance from unfiltered lamps had no effect on height in soybean, sorghum, or corn.

#### **Dry matter production and allocation**

Total plant biomass accumulation (dry weight) is a good indicator of UV-B radiation effects on growth. Total biomass represents a long-term integration of all biochemical, physiological, and growth parameters. Therefore, even subtle UV-B induced effects on physiological processes could accumulate and result in significant effects on biomass. Since plant biomass data are easily obtainable, it is not surprising that a number of studies (Tab. 3) have included the effects of UV-B radiation on dry matter production and its allocation into component plant organs. These studies show that total plant dry weight is often substantially reduced by UV-B. Brandle et al. (1977) found that dry weight in pea was significantly reduced after only 9 days of UV-B irradiation. Although large species differences exist (Tab. 3), reductions in total biomass are often accompanied by substantial modifications in the partitioning of biomass into component plant organs. In dicotyledons, a greater proportion of biomass is allocated into leaves (despite an absolute reduction in leaf area) and less into stems and roots. In species such as soybean, bean, pea, and cucumber, the increase in the proportion of dry weight found in leaves is the result of an increase in SLW. This trend is not nearly as clear in monocotyledons, where a multitude of species specific responses are found. As with the other morphological and anatomical characteristics previously examined, the greatest effects on total dry weight accumulation and biomass reallocation were reported in growth chamber (Biggs and Kossuth 1978) or shaded greenhouse (Vu et al. 1978, Van et al. 1976) studies. Teramura (1980), using various combinations of UV-B and PAR levels found that soybean dry weight and the allocation into various organs were increasingly affected as growth PAR levels decreased. This indicated that UV-B induced reductions in total biomass were magnified under low PAR regimes.

Tab 3 Effects of ultraviolet-B radiation on greenhouse and growth chamber grown plants. \*, refers to citations in Tab 2.

Crop	UV effects on total plant dry weight		
	Increase	Decrease	No change
Wheat	8*	8, 36	8, 21
Rice		8	8, 45
Corn		8, 50	5, 42, 43, 45, 57
Barley		8, 57	42
Oats	8	5, 43, 45	
Sorghum		8, 45	5
Soybean		5, 8, 9, 21, 36, 37, 43, 45, 49, 50	
Cotton			2, 8, 21
Beans		8, 42	21, 57
Peas	8	8, 12, 43, 45, 50	
Rye		8, 45	
Tomato	6	8, 45	21
Millet		8	21, 43, 45
Peanut	8		5, 43, 45
Radish	8	57, 58	21, 42
Cucumber	6	8	21
Squash		8	
Cabbage		8, 45	
Collards		5, 8, 45	
Onion			8
Lettuce		8	21
Celery	8		
Carrots	8		
Parsnip			8
Eggplant	8		
Bell pepper			8
Chard		8	
Okra		8	
Asparagus			8
Artichoke	8		
Sunflower	8		
Broccoli		8	
Brussel sprouts		8	
Cauliflower		8	
Kale		8	
Kohlrabi		8	
Mustard		8	
Rutabaga		8	
Pumpkin		8	
Watermelon		8	
Cantaloupe		8	
Chufa	8		
Rhubarb		8	

In a field study with unfiltered lamps, Ambler et al. (1978) found that massive UV doses simulating up to an 8-fold increase in ambient levels, had no effect on aboveground dry weight production in squash (*Cucurbita maxima* L.), bean, or corn; however, reductions were noted for broccoli (*B. oleracea* L. cv. botrytis) and sugar beet (Tab. 4). Also using unfiltered lamps, Hart et al. (1975) found no effect on corn, sorghum, soybean or peanut. Biggs and Kossuth (1978) on the other hand, reported total dry weight reductions in field grown corn, pea, tomato and mustard (*Brassica juncea* cv. crispifolia) irradiated with filtered lamps. Interestingly, plant dry weight was somewhat stimulated by the highest UV-B

irradiance in potato although this stimulation cannot presently be explained. In sensitive crops, leaf biomass proportionately increased, while stem and sometimes root biomass decreased. The trends observed in this field study were remarkably similar to those found in growth chambers. In another field experiment, Caldwell et al. (1975) found that aboveground dry weight was reduced in barley and pepper (*Capsicum annum* L.), while belowground reductions were observed in soybean, pepper and corn. Alfalfa (*Medicago sativa* L.) and tomato were apparently unaffected by the relatively large UV-B irradiance (simulating 50% ozone depletions) used in that study.

Tab 4 Effects of UV supplementation on field grown crops. 0, unaffected, +, stimulated and -, decreased relative to controls. 1, unfiltered BZS-CLG and FS-40 sunlamps, 2, FS-40 sunlamps filtered with 0.13 mm cellulose acetate, 3, FS-40 sunlamps filtered with 0.13 mm Kodacel TA401, 4, unfiltered FS-40 sunlamps.

Crop	UV effect on total dry weight			
	Ambler et al. (1978) <sup>1</sup>	Biggs and Kossuth (1978) <sup>2</sup>	Caldwell et al. (1975) <sup>3</sup>	Hart et al. (1975) <sup>4</sup>
Rice		0		
Corn	0	-	+	0
Potato		+		
Sorghum	0			0
Soybean	0		-	0
Sugar beet	-			
Beans	0			
Cowpea	0	-		
Tomato		-	0	
Peanut		0		0
Pepper			-	
Barley			-	
Tobacco				0
Millet				0
Cabbage				0
Squash	0	0		
Broccoli	-			
Mustard		-		

#### Crop yield

Nearly all of our information on the effects of UV-B radiation on crops comes from either growth chamber or greenhouse studies. Owing to space limitations, it is impractical to grow plants to reproductive maturity in such facilities. Of all the components of dry matter production, allocation into reproductive organs or crop yield is of major interest in crop species. It is the key factor in our assessment of the impacts of a partial stratospheric ozone depletion. Yet surprisingly, only a handful of studies exist where plants were grown to a stage with harvestable fruit (Tab. 5), and none of these are readily available to the scientific community. With the exception of leafy vegetables, whose yield may perhaps be assessed in the confinement of controlled environments, our understanding of UV-B radiation effects on crop yield is based on only a few field trials and on a limited number of crops. Hart et al. (1975) grew 10 crop species [tomato, sweet pepper, corn, sorghum, soybean, peanut, cotton, tobacco (*Nicotiana tabacum* L.), millet and cabbage] under unfiltered (FS-40) sunlamps, providing a very large UV radiation (UV-B and UV-C) supplement. Despite this massive UV dose, they only found a significant reduction in fruit number in pepper, and only for one of the two experimental growing seasons. Yield was unaffected in the 9 other crops. In a similar field experiment, Ambler et al. (1978) used unfiltered (BZS-CLG and FS-40) sunlamps to test 8 crops (squash, bean, corn, sorghum, soybean, sugar beet, broccoli and cowpea). Based upon their biological effectiveness ( $A_{\Sigma 9}$  weighting function),

these lamps produced UV enhancements up to 8-fold greater than normally incident in the field. Again, despite the high UV irradiance, yield was significantly reduced only in broccoli. Esser (1980) conducted a field experiment in the Federal Republic of Germany using filtered (Schott WG 305, 2 and 3 mm) and unfiltered (Philips TL 40/12) sunlamps over 6 crops (potato, spinach, bean, radish, barley, and cabbage). The radiation from filtered lamps simulated UV-B enhancements resulting from less than 10% ozone depletions and had no significant effect on yield in any of the crops tested. In fact, yield was slightly stimulated in most crops receiving the additional UV-B radiation. Unfiltered lamps which produced irradiances simulating up to 40% ozone reduction, reduced yields in potato (tubers) by as much as 41%, spinach (leaves) by 66%, cabbage (leaves) by 49%, and bean (pods) by as much as 75%. However, the emission from these unfiltered lamps also included UV-C radiation. Because of the strong wavelength specificity of biological responses, the large effects resulting from unfiltered lamps are most likely grossly exaggerated and therefore, interpretations from studies using unfiltered lamps should only be made with utmost caution.

An interesting field study was conducted by Bartholic et al. (1975) in Florida. Three crops (corn, bean, and tomato) were grown under panels covered with either UV-B absorbing (Mylar) or UV-B transmitting (polyethylene) films. Plants grown under the Mylar panels had the direct beam component of the naturally occurring UV-B irradiance filtered out, but still received the diffuse component. This diffuse component

Tab. 5. A summary of field studies on the effects of supplemental UV radiation on crop yield. Values represent the percentage change from controls: 1, unfiltered sunlamps; 2, ambient UV-B irradiance; 3, cellulose acetate filtered sunlamps; 4, values not given

Crop	Hart et al. (1975)	Bartholic et al. (1975)	Ambler et al. (1978)	Biggs <sup>1</sup> and Kossuth (1978)	Esser <sup>1</sup> (1980)
Rice				0	
Corn	0	+8%	0	0	1
Potato				0	-40%
Sorghum	0		0		
Soybean	0		0		
Sugar beet			0		
Beans		0	0		-75%
Cowpea			0	-26%	
Tomato	0	0			
Peanut	0			0	
Pepper	0/-24				
Cotton	0				
Tobacco	0				
Millet	0				
Cabbage	0				-49%
Squash			0	-69%	
Broccoli			-45%		
Radish				0	
Mustard				-19%	
Spinach					-66%

contains nearly 50% of the total incoming UV-B radiation. They found no yield differences in bean or tomato, but yield in corn was significantly greater under the polyethylene panels (Tab. 5). This apparent stimulation in yield was at least partially the result of greater insect infestation under the Mylar panels.

Biggs and Kossuth (1978) used filtered (0.13 mm cellulose acetate) sunlamps (FS-40) to supplement natural UV-B radiation in the field. Unlike the previously described studies, they used an artificial soil medium in raised beds and grew 9 crops (potato, tomato, corn, pea, peanut, squash, rice, mustard, and radish) under a gradient of increasing UV-B radiation. Total yield in corn, rice, radish, peanut, and potato was unaffected by enhanced levels of UV-B, although there was some evidence of qualitative changes in tuber and fruit sizes in potato and peanut, respectively. In mustard, the only leafy crop investigated, enhanced UV-B resulted in significant reductions in leaf dry weight and therefore yield. In squash, total fruit weight decreased, while both total fruit weight and number diminished in pea. UV-B irradiation also resulted in reductions in total fruit production and average fruit weight in tomato. Although the results from this study suggested that UV-B radiation from filtered lamps was apparently effective in reducing yield in 4 out of 9 crops, the magnitude of yield reduction was not generally related to UV-B dose. In 2 of the 3 crops showing fruit yield reductions, the highest UV-B irradiance had only a small effect, while a much lower one produced substantial effects. As was the case in the study by Bartholic et al. (1975), some of these inconsistencies were produced by

insect infestation (R. H. Biggs personal communication).

Until the discrepancies can be resolved, all the field experiments to date have only limited use. As can be gathered from these disparate studies, much more information is needed before a reliable assessment can be made on the effects of a partial ozone depletion on global crop productivity.

#### Response differences to UV-B radiation

Prior to the organization of the Climatic Impact Assessment Program (CIAP) by the U.S. Department of Transportation (Nachtwey et al. 1975), very little was known about the effects of UV-B radiation on plants. In fact, nearly all the studies available up to that time utilized broadband UV-C radiation or monochromatic UV-C radiation, principally 254 nm. Unfortunately, known photobiological responses to 254 nm can only be used for comparative purposes and not for extrapolation or quantitative assessments of UV-B radiation enhancements arising from projected ozone reductions. Not only do quantitative differences in response occur between the two wavebands, but there has been some suggestion that qualitative differences might also be present (Nachtwey 1975). Therefore, one of the primary objectives of CIAP was to empirically determine UV-B sensitivities in a range of different plant and crop species. As a result of this and other continuing efforts, over 45 different crop species have been screened under a diverse range of environmental conditions in growth

chambers and greenhouses (Tab. 3), and in a limited number of field experiments (Tab. 4). This number would approximately double if crop cultivars and other economically important plant species are also considered.

#### Interspecific differences

There are large interspecific response differences to UV-B radiation in terms of total biomass production (Tabs 3 and 4). Some species are resistant to UV-B radiation, most are sensitive to a degree, while growth in others is apparently stimulated. In an extensive screening experiment conducted in growth chambers including over 40 crop species and 30 cultivars (Biggs and Kossuth 1978), about 30% of the crops tested were either unaffected or stimulated by UV-B radiation, another 20% were extremely sensitive, and the remainder were intermediate in sensitivity, based upon total dry matter production. Considering all other plant characteristics which were influenced by UV-B radiation, such as leaf area, height, biomass partitioning pattern, etc, there apparently is an enormous array of UV-B responses expressed by different crop species. Obviously, a multitude of morphological, anatomical and physiological processes all act in concert to provide different species sensitivities, including differences in cuticle thickness, the presence of UV absorbing pigments, changes in SLW, leaf reflectivity, crop or leaf canopy development, etc.

Regardless of these species specific response differences, however, a few broad generalizations can be made, given the same treatment conditions. Monocotyledons as a whole, seem to be less affected by UV-B radiation than dicotyledons (Van and Garrard 1975, Teramura 1980, Tevini et al. 1981). It has been suggested that this difference might be partially due to the vertical leaf orientation, protective basal sheath, and the protected meristematic region in monocotyledons (Van and Garrard 1975). At least one study (Basiouny et al. 1978) concluded that crops with the  $C_4$  photosynthetic pathway were more affected than those with the  $C_3$  pathway. In terms of plant height and total biomass accumulation, those researchers found that neither of the  $C_4$  crops investigated (sorghum and corn) was affected by UV-B irradiation, while all the  $C_3$  crops (collard, oats, peanut, and soybean) had at least one of these characteristics affected. Finally, some plant families show relatively uniform responses. For example, 8 of 10 crops belonging to the Cruciferae were extremely sensitive to UV-B radiation while the Poaceae was relatively resistant (Biggs and Kossuth 1978).

#### Intraspecific differences

In addition to the sizable interspecific differences in UV-B radiation response, there is an appreciable in-

traspecific response difference (Tab. 3). Many of the crops listed showed a variable response to UV-B radiation in terms of dry matter production. Although some of this represents differences in UV-B irradiance or treatment conditions between individual studies, it also reflects cultivar response differences. Large cultivar differences in UV-B response have been reported in soybean (Biggs et al. 1981, Vu et al. 1978), cotton (Ambler et al. 1975), bean (Bennett 1981, Dumpert and Boscher 1982), collard and cabbage (Van et al. 1976, Garrard et al. 1976), wheat, barley, corn and rice (Biggs and Kossuth 1978), and spinach (Dumpert and Boscher 1982). In a growth chamber study of 19 soybean cultivars, Biggs et al. (1981) concluded that 20% were extremely sensitive to UV-B radiation, 20% were relatively resistant, and the remainder were intermediate in sensitivity. Surprisingly, these proportions of sensitive and resistant cultivars are very similar to those found between species, indicating that a tremendous range of intraspecific variability to UV-B radiation is present in the soybean germplasm. Currently, the reasons for the cultivar variability are not completely understood, nevertheless it does suggest that there is a potential for genetically modifying future cultivars to minimize the deleterious effects of a global ozone depletion.

*Acknowledgements* – The author would like to thank Irv Forseth, Roman Mirecki and John Lydon for their comments on an earlier version of this manuscript. Also many thanks to Inez Miller for her careful typing. This work was supported by the United States Environmental Research Laboratory in Corvallis, Oregon (CR 808-035-020), and grants from the Graduate School and Provost to the author. Scientific Article No. A-3368, Contribution No. 6440 of the Maryland Agricultural Experiment Station, Department of Botany. Although the work described in this article has been funded in part by the United States Environmental Protection Agency, it has not been subjected to the Agency's required peer and policy review and therefore does not necessarily reflect the view of the Agency and no official endorsement should be inferred.

Travel to the international workshop held in Delhi, India, was supported by N. S. F.

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