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Martyn M. Caldwell

Stephan D. Flint

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## STRATOSPHERIC OZONE REDUCTION, SOLAR UV-B RADIATION AND TERRESTRIAL ECOSYSTEMS

MARTYN M. CALDWELL and STEPHAN D. FLINT

*Department of Rangeland Resources and the Ecology Center, Utah State University, Logan, Utah  
84322-5230, U.S.A.*

**Abstract.** Stratospheric ozone reduction is occurring and will continue to increase in magnitude into the next century. Yet, the consequences for terrestrial ecosystems of the increased solar UV-B (280–320 nm) radiation resulting from total column ozone reduction are not understood. Based on studies of higher plant response to UV-B, several possible consequences for ecosystems include decreased primary production, altered plant species composition, and altered secondary chemistry with implications for herbivory, litter decomposition and biogeochemical cycles. However, like the assessment of increased atmospheric CO<sub>2</sub>, extrapolation from studies with isolated plants to ecosystem function is very tenuous at best. Very few UV-B studies have dealt with multispecies systems. Most of the UV-B research in the past two decades (since the first suggestions of ozone reduction) has been conducted as short-term experiments in growth chambers and greenhouses where the unnatural spectral balance of radiation can lead to unrealistic conclusions. Technical difficulties in suitable measurement and manipulation of UV-B radiation also complicate the conduct of reliable experiments. This essay surveys and categorizes some 300 papers from the past 20 years on this subject, draws general conclusions from the research and offers some recommendations with respect to ecosystem consequences.

### 1. Introduction

Documented global atmospheric changes present some of the most compelling questions for the ecological community. Forecasting ecosystem consequences of these changes is an elusive, but necessary, goal. Increasing atmospheric CO<sub>2</sub> and increases in other greenhouse gases have received the most attention. Stratospheric ozone reduction – not only the dramatic Antarctic ozone hole, but the general decline at temperate and high latitudes – presents a rather different set of questions. Since approximately 90% of the total atmospheric ozone column is in the stratosphere, changes at these high altitudes largely determine the total column radiation attenuation properties in those wavelengths where ozone is the principal absorber (Madronich, 1993). Therefore, the primary concern is the increased penetration of solar UV-B (280–320 nm) radiation to the earth's surface. This portion of the solar UV spectrum is particularly effective in eliciting photochemical reactions. Thus, even though small quantities of radiation are involved – less than  $\frac{1}{2}\%$  of the total solar flux reaching the earth's surface (Blumthaler, 1993) – there can be biologically significant effects of this radiation.

In this essay, we wish to assess the current state of UV-B research for terrestrial ecosystems and draw some parallels with analogous research addressing the elevated CO<sub>2</sub> question. There is a fundamental difference in that CO<sub>2</sub> is primarily a resource for vegetation while UV-B may be better classified as a stress or some-

times a source of information for plants. Nevertheless, the global nature of these atmospheric-change problems and the need to assess potential ecosystem-level consequences make the analogy worth pursuing.

Although the title involves terrestrial ecosystems, the research to date has been conducted almost exclusively with higher plants. The general sentiment is that insects and other animals that are routinely exposed to sunlight are well protected by pigments, fur, exoskeletons, etc. This certainly bears greater scrutiny in the future. For example, some amphibian eggs in exposed locations can be damaged by solar UV-B radiation (Blaustein *et al.*, 1994). As discussed later, there are potential indirect effects of UV-B on herbivores and detritivores caused by changes in the chemical and physical properties of plants. These indirect effects on consumers and detritivores mediated by the vegetation are likely to be more important in ecosystem function than direct effects of UV-B on these organisms.

Some perspective on atmospheric processes and anticipated events in the coming decades will first be presented. This will be followed by a short discourse on latitudinal gradients and then some commentary on technical problems involved in UV-B measurement and manipulation in experiments with plants. An overview of research thus far conducted and its pertinence to ecosystem analysis will follow next. Finally, some generalizations about common findings from the research and recommendations for the future are offered.

## 2. Will Ozone Continue Decreasing?

The Montreal Protocol and the subsequent convention agreements reached by the principal treaty parties may well be the most successful international accord on environmental protection thus far achieved. Recent measurements also confirm that the growth rates of some of the most offending chlorofluorocarbons (CFC<sub>11</sub> and CFC<sub>12</sub>) are slowing (Elkins *et al.*, 1993). Nevertheless, the chlorine and bromine loading in the atmosphere will continue to increase for about a decade before a slow decline begins, and chlorine in the stratosphere will be above the abundance at which the Antarctic ozone hole formed for about a century! This will be further complicated by the detrimental effects of increasing CH<sub>4</sub>, NO<sub>x</sub>, aerosols, and CO<sub>2</sub> in the atmosphere (e.g. Waters *et al.*, 1993). Thus, stratospheric ozone reduction will be very much an issue in the coming several decades.

Furthermore, though much has been learned concerning stratospheric ozone behavior, the history of atmospheric developments in the last two decades has been marked by several unanticipated events. The Antarctic ozone hole was the most dramatic, but in the last few years general ozone reduction at temperate latitudes has been much greater than predicted by atmospheric models (Gleason *et al.*, 1993). Unequivocal explanations have not yet become available. In short, though long-term predictions are somewhat favorable, in the coming decades considerable uncertainty remains. Thus, ecological consequences of these changes need to be assessed.

### 3. Stratospheric Ozone and Solar UV-B Radiation Vary Considerably over the Earth

Unlike tropospheric CO<sub>2</sub> which is reasonably uniform over the globe, stratospheric ozone is not. Although much of the stratospheric ozone forms at low latitudes, stratospheric circulation patterns result in greater accumulations of the ozone at higher latitudes. There are also seasonal variations; ozone column thickness reaches a maximum in the early spring and a minimum in the late fall (e.g., Frederick *et al.*, 1989).

In addition to the latitudinal gradient of stratospheric ozone, prevailing solar angles at different latitudes largely determine the solar UV-B under cloud-free conditions. When the sun is closer to the zenith, there is a shorter pathlength for solar radiation to penetrate through the atmosphere and, therefore, there is less attenuation than when the sun is further from the zenith. The combination of smaller solar zenith angles and less column ozone at lower latitudes results in much greater solar UV-B flux at these latitudes – especially at the shorter UV-B wavelengths. (As discussed later, radiation at the short UV-B wavelengths is most effective in biological reactions.)

The latitudinal gradient of solar UV-B has the important result that a small relative change in ozone column at low latitudes can result in the same absolute increment of solar UV-B as a massive relative ozone decrease at high latitudes. For example, at the time and location of the Antarctic ozone hole, a 40 to 50% depletion of the ozone column results in about the same absolute increase in daily UV-B radiation flux as less than 5% ozone depletion in the springtime at 30° latitude (these computations include a weighting function to describe general biological effectiveness of the radiation (Caldwell, 1971) as discussed later). An important ecological question, however, is whether it is the absolute or relative increase in solar UV-B that is important for organisms. Organisms may be adapted to levels of solar UV-B at the latitudes where they exist and changes relative to these levels may be most pertinent. There are a few data sets to support this notion (Caldwell *et al.*, 1982; Barnes *et al.*, 1987), but such evidence is far too limited to be considered robust. This is an important question in future assessments.

### 4. UV-B Manipulation, Dosimetry and Weighting Functions

This essay is not meant to deal comprehensively with technical aspects of UV-B research, however, it is important to convey an impression of the difficulties involved. These difficulties are in part purely technical and in part a matter of training biologists to appreciate and deal with these technical issues. Biologists who conduct whole-plant experiments find that light measurement and manipulation are rather routine and straightforward. The introduction of an integrating dosimeter for total photon flux in the visible waveband (400–700 nm) by Biggs *et al.* (1971) was a very useful contribution for plant scientists. With this ‘quan-

tum sensor', one can easily measure what is commonly termed 'photosynthetically active radiation – PAR' or 'photon flux density – PFD'. An error analysis by McCree (1981) shows that the errors involved in using the quantum sensor with sunlight and various lamps are small. Also, he showed that the discrepancy between the true photosynthetic action spectrum and the quantum sensor spectral sensitivity approximating total photon flux is usually not serious. Thus, with relative impunity, the plant biologist can easily make PFD measurements and concentrate on other aspects of his/her research.

Unfortunately, in the UV-B spectrum, measurement and expression of biologically meaningful UV-B are much more complicated and prone to errors (Diffey, 1986). The lamps and filters generally available for manipulating the UV-B in plant experiments do not provide ideal simulations of solar UV-B (Caldwell *et al.*, 1986). Furthermore, there are problems with optical degradation, aging and sensitivity to environmental factors such as temperature.

Briefly, the basis of these problems lies with the absorption coefficient of ozone which drops by orders of magnitude in the UV-B waveband (Stamnes, 1993). These absorption characteristics determine how the solar spectrum reaching the earth's surface is truncated in the UV-B waveband and how ozone column reduction results in a very wavelength-specific increment of solar UV-B. Within the UV-B, ozone column reduction is only important in a waveband of about 25 nm – between 290 and 315 nm. At shorter wavelengths, absorption by ozone is so great that a small fraction of the present ozone column is sufficient to block all radiation completely; at longer wavelengths, it is so weak that decreases of ozone effect inconsequential increases of UV flux. Within this 25-nm waveband, the solar irradiance decreases by more than four orders of magnitude as a result of ozone absorption. With ozone reduction, the relative enhancement of UV-B is also highly wavelength dependent (Figure 1).

The additional radiation resulting from ozone reduction appears trivial if only considered as a fractional increase in total solar flux reaching the earth. However, it becomes important if radiation at the shorter UV-B wavelengths, which increases the most with ozone reduction (Figure 1), is more biologically meaningful than the radiation at the longer UV-B wavelengths. Indeed, the biological effectiveness of most reactions to UV-B does increase considerably with decreasing wavelength – sometimes by orders of magnitude (Caldwell *et al.*, 1986). To quantify this, the spectral irradiance in the UV is usually weighted by a function describing the biological effectiveness. Analogous to a quantum sensor for measuring PFD, dosimeters (e.g., Berger, 1976; Diffey, 1986) have been devised for obtaining a weighted integrated measure of 'effective' UV-B (the weighting function usually is that describing sunburning of human skin). Such dosimeters can deviate in spectral responsivity from the desired function (Smith and Ryan, 1993). Even if these dosimeters perform flawlessly, the quantity obtained is confined to the built-in weighting function and this cannot be easily extrapolated to UV-B weighted with other biological functions. This is particularly a problem when such dosimeters

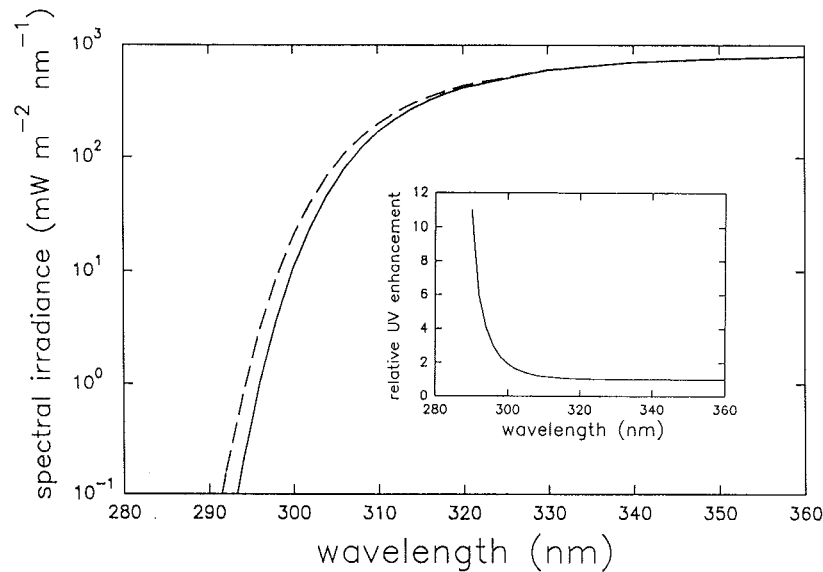


Fig. 1. Solar spectral irradiance (direct beam + diffuse) computed for normal ozone column thickness and solar angle appropriate for midday in the summer at temperate latitudes. The dashed line represents the irradiance for the same conditions, but with a 20% ozone column reduction. The inset shows the relative factor by which irradiance is increased due to ozone reduction at different wavelengths.

are used to measure radiation from different sources – e.g., from the sun and from lamps.

Alternatively, one can measure the spectral irradiance, wavelength by wavelength. This is certainly the most desirable, but an instrument that can do this adequately in the solar UV-B spectrum involves much more demanding (and expensive) characteristics than if only measuring in the visible spectrum. The primary reason for this is the orders-of-magnitude change in solar flux in this part of the spectrum (Kostkowski *et al.*, 1982).

Whether spectral irradiance data are collected or UV-B is estimated with a dosimeter, the issue of the appropriate biological weighting function must be addressed. These weighting functions are involved both in assessing and manipulating UV-B. Small differences in these functions can result in large differences in the radiation determinations since both the spectral irradiance and many of the weighting functions change by orders of magnitude in the UV-B. Use of weighting functions will not be addressed further here, but other sources discuss these issues (Caldwell *et al.*, 1986; Madronich, 1993).

Manipulating UV-B in biological studies involves either filtering sunlight or use of UV lamps and filters that are prone to many limitations and problems. Aging and temperature dependency of lamps (Adamse and Britz, 1992; Diffey, 1988) photodegradation of filters (Miller *et al.*, 1992; Middleton and Teramura, 1993a) and geometrical constraints (Björn and Teramura, 1993) are not always

appreciated or monitored. Since rather small amounts of energy are involved in these manipulations and the UV-B phenomena are so wavelength specific, small discrepancies can result in substantial problems.

### 5. Overview of Plant Research Involving UV-B

Although photobiological research with short-wavelength UV-C (< 280 nm) has a long history, most of the work dealing specifically with UV-B has occurred in the last two decades. This was stimulated by the first concerns of stratospheric ozone layer reduction in the early 1970's. There are several recent reviews of much of this literature (Caldwell *et al.*, 1989; Tevini and Teramura, 1989; Teramura, 1990; Tevini, 1993; Caldwell and Flint, 1994). In this section we present a summary of the categories of research conducted, draw some generalizations from the literature and discuss the relevance of this body of knowledge for assessing consequences of ozone layer reduction for terrestrial vegetation. For this survey, 297 papers have been examined. Even compared with the approximate 1200 papers on the issue of plant response to elevated CO<sub>2</sub> where so much more work has been conducted (Körner, 1993), this appears to be a substantial number of papers dealing with UV-B. Upon closer examination, this collection of papers provides information on potential effects of elevated UV-B on plants and mechanisms of UV action, but relatively little insight into the larger ecological questions relevant to this environmental problem. Unfortunately, as with the elevated CO<sub>2</sub> problem, the studies that contribute most to realistically assessing the elevated UV-B problem are the most expensive and time consuming. Thus, the literature is primarily composed of short-term experiments with limited realism for ecological questions (Figure 2).

In the 297 papers mentioned above, there are 330 experiments reported (Figure 2). Of these, almost half (47%) of the experiments have been conducted with isolated plants in growth chambers or greenhouses. Another nearly 33% involved work at the cellular and organelle level, assessments of leaf optical properties and theoretical or review papers. Of the few studies conducted in the field, only a few have involved plants in canopies and fewer still with mixed-species canopies. (The classification of 'field studies' is taken very liberally and includes any research conducted with sunlight, even if the plants were growing in pots, or in special chambers. Such experiments either involved manipulation of sunlight with filters or supplemental UV-B from lamp systems – usually without provision to adjust the lamp UV-B output as conditions change.) Clearly, there is a pressing need for research dealing with more complex systems, e.g., species mixtures growing in the normal soil profile over long periods of time.

The duration of experiments ranges from a few hours to several years, but most are rather short term. In a survey of greenhouse and growth chamber studies in the past 4 years and all field studies in the past 20 years, more than 90% lasted only a few months or less (Figure 3). This is particularly the case for greenhouse and growth chamber experiments. In a 6-year field study of soybeans (Teramura





*et al.*, 1990a) and a 5-year field study of competition between wheat and wild oat (Barnes *et al.*, 1988), the effects of supplemental UV-B varied among years. Though in most years the effects of UV-B were apparent, in a few quite dry years in both studies, the effects of UV-B were not evident. In both of these studies, these annual plants were replaced each year. Very little work has dealt with perennials, especially trees. A three-year field study of *Pinus taeda* seedlings indicated that apparent growth inhibition due to elevated UV-B tended to accumulate over the three-year period (Sullivan and Teramura, 1992).

How plants respond to UV-B is dependent on how much UV-B they receive and under what environmental conditions the plants grow and are irradiated. Early in the history of this research it became apparent that plants growing in the field were much less sensitive to UV-B than when grown in greenhouses or growth chambers. There may be several reasons for this, but experiments specifically designed to investigate the influence of PFD level on UV-B sensitivity showed that UV-B effects were less pronounced if plants were under higher PFD (Teramura, 1980; Teramura *et al.*, 1980; Warner and Caldwell, 1983; Mirecki and Teramura, 1984; Latimer and Mitchell, 1987; Cen and Bornman, 1990; Kramer *et al.*, 1991; Kumagai and Sato, 1992). More recently a field study using a combination of UV-emitting lamps and filters indicated that both higher PFD and UV-A had mitigating effects on UV-B reduction of plant growth (Caldwell *et al.*, 1994). Although they did not specifically test the effect of different levels of UV-A and PFD on UV-B sensitivity, Middleton and Teramura (1993b) showed that UV-A could exert both positive and negative effects on plant growth and some physiological characteristics in a greenhouse study. Usually, the UV-A is not reported in greenhouse and growth chamber experiments. However, since some of the UV-A is removed by greenhouse glass and the lamps in many growth chambers do not emit a large flux of UV-A, fluxes of UV-A comparable to those in sunlight are not anticipated (Middleton and Teramura, 1993b).

In many growth chamber and greenhouse experiments the ratios of UV-B: PFD used are considerably higher than in the field. In greenhouse experiments, this is in part attributable to cloud cover in which case the UV-B-emitting lamps are usually not adjusted for lower output during cloudy periods. Of course, this can also take place in field experiments in which UV-B lamps are used. There are electronic modulation systems available which can automatically accomplish this adjustment of UV-B lamp output to keep a realistic ratio of UV-B : UV-A : PFD as conditions change during the day (Caldwell *et al.*, 1983a; Björn and Teramura, 1993; McEvers *et al.*, 1993), but these have not been widely used.

To provide some perspective on how the average daily UV-B and PFD employed in greenhouse and growth chamber experiments relate to the values measured in the field, a brief survey is given in Figure 4. Forty papers describing growth chamber UV-B experiments published between 1990 and October, 1993 were examined for ratios of UV-B : PFD employed in the experiments. Of these, only 14 reported enough information to determine the daily UV-B and PFD used. Since some of

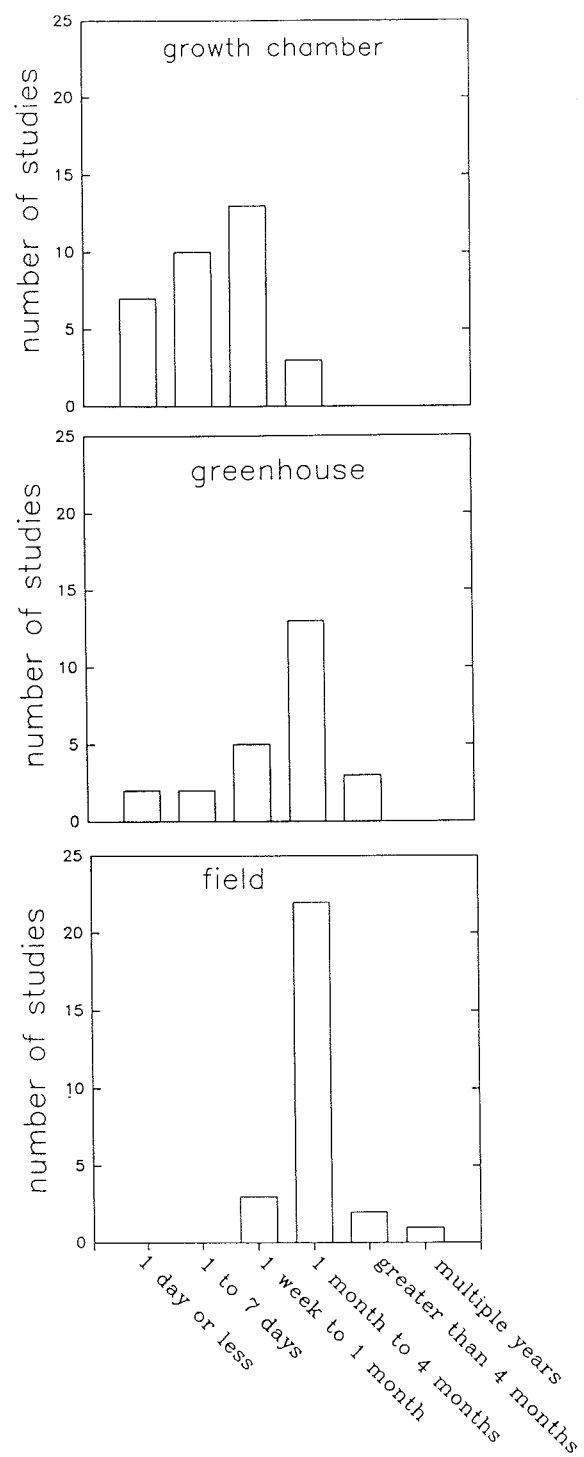


Fig. 3. Frequency histograms of experiment duration for UV-B studies conducted with plants. A sample of 33 growth chamber and 24 greenhouse experiments published between 1990 and October, 1993, and all available field UV supplementation studies conducted since 1972 (23 papers reporting 28 different studies) are included in these diagrams.

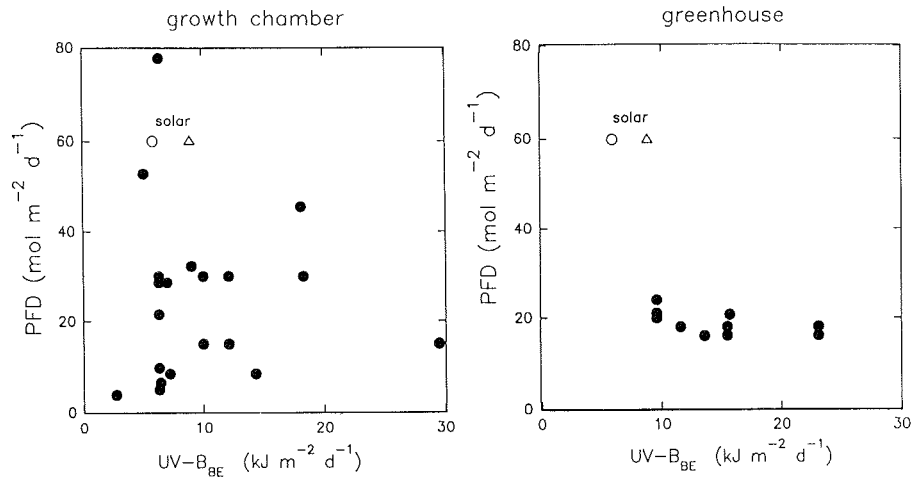


Fig. 4. Average daily integrated biologically effective UV-B using the generalized plant action spectrum weighting function (Caldwell, 1971) normalized to 300 nm ( $UV-B_{BE}$ ) and total photon flux in the 400–700 nm waveband (PFD) employed in growth chamber and greenhouse experiments ( $\bullet$ ). For comparison, measured solar  $UV-B_{BE}$  and PFD on a clear day (3 August 1993) at 1450 m elev. and 41° N latitude ( $\circ$ ) and the corresponding value computed (using the measured values as a basis) for a 20% reduction of the ozone column ( $\triangle$ ). The same papers as surveyed for Figure 3 were used in this depiction.

these papers included multiple treatments, there is a total of 20 data points in Figure 4. Similarly, for greenhouse experiments during the same period, only 6 (out of 27) reported integrated daily PFD and the daily UV-B employed. Again because of multiple treatments, ten data points are available. (We feel simply reporting the maximum midday values of PFD in greenhouse experiments does not provide a useful indication of the daily average values.) Even though maximum PFD in growth chambers may not be particularly great, in some experiments with sufficiently long daylengths, the integrated total-day UV-B : PFD ratio was close to that of the natural environment. However, in most of these experiments the UV-B : PFD ratios were far from those experienced by plants in the field. The levels of UV-B and PFD in Figure 4 and the generally low UV-A in greenhouse and growth chamber experiments leads us to suggest that many such experiments may have substantially exaggerated plant sensitivity to UV-B.

Field UV-B experiments have basically been of two types: UV-exclusion and UV supplementation. Exclusion experiments are the more straightforward of the two since this is only a matter of removing at least a portion of the UV from sunlight by filters. A control for similar microenvironmental influence of the filters is normally accomplished by use of a UV-transparent filter material. Such experiments have been attempted in one form or another for much of a century (Caldwell, 1971). These are appealing in that comparatively little expense is involved and one is not encumbered by many of the problems in using UV-B lamp supplements. If

they are properly conducted and if they indicate effects of the UV-B exclusion, or attenuation, they provide convincing evidence that UV-B under current conditions is influential. If such exclusion experiments do not show effects, they are less meaningful with respect to the ozone reduction problem since one does not know if additional UV-B might exert an influence. Plants may easily accommodate present UV-B levels, but it is then not clear what consequences increased UV-B flux might have in the event of ozone column reduction.

Field UV-B supplementation experiments involve UV-B-emitting lamps used along with the normal solar radiation. (As mentioned earlier, these ideally should be modulated so as to automatically vary in output as the background solar radiation changes.) Field supplementation experiments have only been conducted in a few locations. These have indicated reduced yield in some cases (e.g., Teramura *et al.*, 1990a). However, when compared with experiments in growth chamber and greenhouse conditions, they often have shown that plants exhibit less UV-B damage to photosynthesis and growth, and sometimes no damage was evident (Flint *et al.*, 1985; Beyschlag *et al.*, 1988; Sinclair *et al.*, 1990).

Other such field experiments have indicated more involved and indirect effects of supplemental UV-B that may be ultimately of considerable ecological significance. An example is the influence of UV-B supplementation on plant species competitive balance. There are many responses to UV-B that are primarily photomorphogenetic in nature. These include changes such as decreased leaf and internode length, increased branching and tillering of grasses and increased leaf thickness (Barnes *et al.*, 1990; Ballaré *et al.*, 1991; Barnes *et al.*, 1993). These changes are often not particularly striking, especially under field conditions. In pure stands of a single species, these changes usually result in no significant change in total shoot production. However, in mixed-species stands, these changes can result in altered competitive balance of the species involved (Gold and Caldwell, 1983; Barnes *et al.*, 1988). Such tests of changes in competitive balance have been conducted with planted mixtures and their respective monocultures. Thus far, tests of competitive balance change in vegetation as occurs in nature have not been reported. We are aware of only one study presently underway that addresses elevated UV-B effects on a natural vegetation community (Björn, personal communication).

Stratospheric ozone reduction is not occurring in isolation, but is taking place concurrently with increasing atmospheric CO<sub>2</sub> concentrations and other factors of global climate change. Only a few short-term experiments have addressed the interaction of elevated UV-B and CO<sub>2</sub> in greenhouse experiments and then generally with very high UV-B levels (Teramura *et al.*, 1990b; Rozema *et al.*, 1990; Ziska and Teramura, 1992; Stewart and Hodginott, 1993, van de Staaij *et al.*, 1993). Although the various species reacted differently, there were not always statistically significant interactions between the CO<sub>2</sub> and UV-B treatments for growth and photosynthesis parameters. When there were significant interactions, they generally were in the direction one might expect, namely that UV-B decreased the stimulation due to high CO<sub>2</sub>, or UV-B depressions of growth or photosynthesis were

ameliorated by high CO<sub>2</sub>. Longer-term field experiments testing these interactions under more realistic UV-B : PFD ratios will be required to probe the ecological significance of the combined changes. However, such experiments are necessarily technically demanding and expensive.

## 6. Some General Results from UV-B Research with Higher Plants

At this point, we draw some generalizations from the 300 papers mentioned above:

1. Irradiation with sufficiently large UV-B doses can result in many primary effects in plant tissues including: Inhibition of Photosystem II function in photosynthesis, DNA damage (particularly formation of cyclobutane thymine dimers), free-radical formation, induction of secondary chemistry alterations (particularly in the shikimic acid pathway) and photomorphogenetic changes.
2. At the whole-plant level, UV-B can cause a reduction in net photosynthesis, growth inhibition, anatomical and morphological and allocation changes, increases in flavonoids, related phenolics and phytoalexins, and inhibition of pollen germination and pollen tube growth. Not all whole-plant phenomena can be considered as damage. Sometimes growth changes or allocation alterations do not result in decreased plant fitness. Some might even be interpreted as positive for the plant (e.g., differences in allocation or secondary chemistry).
3. The link between primary events as listed in 1. and whole-plant phenomena listed in 2. is not well established. For example, it is not clear to what extent DNA damage is involved in whole-plant growth inhibition.
4. Plant species and even genotypes within a species can differ greatly in their response to UV-B. Reasons for this are not clear. Differences in protective UV filtration by pigments or plant structure may explain some of these differences. Also, the degree to which additional UV-B-absorbing pigments are formed upon exposure to higher UV-B has also been correlated with the extent of plant accommodation of more intense UV-B.
5. Graminoids tend to be more resistant to UV-B damage than herbaceous dicots. However, for purely photomorphogenetic changes (which do not result in damage) graminoids tend to be more responsive to UV-B than dicots.
6. The effects of UV-B tend to be more pronounced if plants are growing in low PFD. If the ratio of UV-B : PFD is similar to sunlight, the effects are usually much less apparent. There is also evidence that UV-A can also have strong mitigating effects on UV-B influences, especially if PFD is low. Thus, consideration of UV-B : UV-A : PFD ratios is important.
7. Much of the available research has been conducted with unrealistically high UV-B : PFD ratios (UV-A is usually not specified). Therefore, many of the phenomena listed in 1. and 2. may not be representative of plants in natural field conditions, even with a depleted ozone layer.

8. Yet, even without ozone layer reduction, simply removing or reducing the UV-B in sunlight in simple filtration experiments shows that many plants (especially in seedling stage) are detrimentally affected by solar UV-B.
9. Under more realistic ratios of UV-B : PFD, of the whole-plant phenomena listed in 2., the frequency of effects reported in experiments would be: Induction of more flavonoids (and related UV-B-absorbing compounds) > reduced growth and morphological changes  $\gg$  reduced photosynthesis.
10. Experiments with mixed-species canopies are not common. But, those that have been conducted tend to show that increased UV-B results in shifts in competitive balance of species. This is usually not thought to be the result of differential UV-B damage to plants (since the same UV-B does not usually cause a reduction in growth or production in monocultures of these plants). Instead, the shifts of competitive balance may be due to other phenomena such as altered growth and allocation that change competitive ability of the co-occurring species.
11. Experiments involving plant response to combinations of elevated CO<sub>2</sub> and UV-B are very limited and conducted with high levels of UV-B in greenhouses. These generally indicate either no interactions or that the enhancements of elevated CO<sub>2</sub> on growth and photosynthesis are diminished by high UV-B. These interactions also tend to vary among the few species tested.
12. Other environmental stresses such as water deprivation or nutrient limitations often appear to dampen the response to elevated UV-B – but not always. Only a few reports of interactions between UV-B and other factors such as temperature, ozone fumigation, and heavy metals are available. Therefore, generalizations about such factor interactions are not advisable.

## 7. Ecosystem-Level Implications

Based on information available at this time, we speculate that the effects of elevated solar UV-B will probably not be reflected in reduced primary productivity but rather in species composition changes in nonagricultural ecosystems. Nevertheless, this hypothesis of little change in primary production needs to be rigorously tested. (As mentioned before, one field study using potted plants (Sullivan and Teramura, 1992) did show reduced growth of *Pinus taeda*).

In agricultural systems, there may be a few varieties of certain crops that experience some decline in productivity while other varieties of the same crop species will not be influenced (e.g., studies of soybean varieties – Teramura and Murali, 1986; D'Surney *et al.*, 1993). Where crops compete with weeds or in mixed-species intercropping systems, changes in competitive balance may again be more important than reduced productivity as solar UV-B increases.

Other indirect influences of elevated solar UV-B on ecosystems may be mediated by changes in the secondary chemistry of plant tissues. As mentioned in the foregoing list of generalized results, a frequently reported result in both laborato-

ry and field studies is that elevated UV-B often induces increases in plant tissue flavonoids and related compounds. These are generally considered to be protective compounds for plants in that they strongly absorb in the UV and the increased levels of these compounds have been shown to afford greater UV-B protection (Caldwell *et al.*, 1983b; Tevini *et al.*, 1991). However, other changes in phenolics and other classes of secondary compounds may have importance in altering plant susceptibility to disease and herbivory. Secondary metabolites, such as flavonoids, glucosinolates and terpenoids, can act both as attractants and deterrents to insects and other herbivores (Berenbaum, 1988). Recently, McCloud *et al.* (1992) showed that elevated UV-B altered the ratio of certain furanocoumarins (an increased ratio of psoralen to bergapten) and this was correlated with increased bacterial phototoxicity. This, in turn, would suggest that disease severity might be lessened. In another study, larvae of a lepidopteran caterpillar developed more slowly in early life when reared on plants exposed to increased UV-B and this was attributed to potentiation of phototoxins ingested by the larvae due to UV-B irradiation of the plants (McCloud and Berenbaum, 1994). Enhanced UV-B in some cases exacerbates the impact of fungal infection on higher plants (Orth *et al.*, 1990; Panagopoulos *et al.*, 1992). Phenolic and related compounds can also affect digestibility of plant tissues for herbivores or have regulatory effects on animals (such as 'false hormones'). This line of research as it bears on the solar UV-B question is attracting interest in the research community, but such work is still in its infancy. Attractiveness of plants to herbivores may be altered not only by changes in secondary chemistry, but also by altered tissue morphology such as foliage toughness. A common response of leaves to UV-B is an increase in leaf thickness (Barnes *et al.*, 1990).

There are many other ecosystem-level implications of altered secondary chemical changes (Caldwell *et al.*, 1989). Products of the shikimic acid pathway in plants influence the food quality of agricultural products, and have functions such as insect attractants, regulators of pollen tube growth and signals for symbiotic bacteria. If lignin and other related end-products of this pathway are altered, decomposition rates of plant materials may be changed which, in turn, can have a bearing on biogeochemical cycles.

These implications of altered secondary chemistry and plant morphology on plant diseases, herbivory and decomposition rates are primarily matters of speculation at this time. However, realistic tests of these phenomena in ecosystem-level experiments are needed.

There is limited evidence that UV can alter aspects of plant phenology, e.g., flowering (Kasperbauer and Loomis, 1965; Caldwell, 1968) senescence of foliage (Sisson and Caldwell, 1977), etc. These phenomena have received little attention. As with some of the changes in plant morphology and allocation induced by UV-B, altered phenology of plants in isolation may be of little consequence. However, in an ecosystem context, such changes may alter competitive balance, or relations between plants and their pollinators that, in turn, might change ecosystem composition.

## 8. A Few Recommendations

Ecosystem-level field experimentation is needed to evaluate realistic consequences of increased solar UV-B resulting from ozone column reduction. Vegetation in ecosystems functions differently than plants in isolation and behavior of the former is not easily predicted from the latter. The history of research on the elevated CO<sub>2</sub> question certainly shows that ecosystem-level effects of elevated CO<sub>2</sub> are not easily predicted from experiments with isolated plants (Körner, 1993). If our thesis is correct that the most meaningful consequences of increased solar UV-B are indirect effects as discussed in the preceding section, these can be played out in ecosystem interactions that are not readily envisaged.

The ecosystem-level consequences of other chronic stresses have been investigated in greater detail, e.g., ionizing radiation (Armentano and Woodwell, 1976) or factors leading to forest decline (Schulze *et al.*, 1989). Such work provides examples of ecosystem study, but due to the very different nature of the stresses examined, they cannot be extrapolated to the question of increased solar UV-B radiation.

Given the expense, physical constraints of manipulating UV-B, and time-consuming nature of ecosystem-level study, considerable thought must be given to candidate systems for study. Since few systems can be studied and extrapolation to unstudied ecosystems will be tenuous, a mechanistic line of investigation should be superimposed on ecosystem-level experiments.

Although few would argue with the need for mechanistic understanding of any phenomenon, mechanistic investigation means different things to different investigators. For the elevated UV-B problem, there has already been a considerable effort directed to understanding mechanisms at the photochemical, molecular and physiological levels (see Figure 2). While a few rather specific efforts at these levels may still be useful, a greater emphasis should be placed on mechanisms at the whole-organism and interorganism levels. For example, much is known about the sites and modes of UV-B action on photosynthesis. Though more information might be useful for some purposes, we feel it is more important to establish at the ecosystem-level of study if intact plant photosynthesis is indeed affected under realistic UV-B : PFD ratios for particular ozone reduction scenarios. If primary production or species composition changes occur as a result of UV-B alterations at the ecosystem-level, the reasons for this should be resolved, i.e., mechanisms at the whole-organism or interorganism level. For example, if species composition changes, is this the result of differential damage to photosynthesis or growth? ... or, is this the result of altered plant morphology that translates into altered competition for light or belowground resources? ... or are shifts in secondary chemistry and resulting alterations in disease or herbivory responsible for the altered species composition? Though such 'mechanisms' may be specific to the particular species under study, they provide a basis for modeling changes in other ecosystems. They also provide a basis for judiciously selecting research at more



physiological levels of study. For example, if the altered species composition is the result of differential morphological changes for the principal species, what is the physiological/photobiological basis of these differences?

Some modes of UV-B action at the ecosystem-level may become first apparent by following population-level parameters. For example, little is known thus far about the effects of UV-B on plant reproductive biology studied at the level of pollen or ovule. While work is needed in this area, tracking population-level indicators of reproductive success in ecosystem-level studies may provide the best indication of UV-B effects on reproduction. Again, if these become apparent, more mechanistic study is in order as described above.

While we suggest that ecosystem-level study be the focus of research designed to evaluate the stratospheric ozone problem, there are good reasons to also include specific studies under more reductionist conditions. Apart from the targeted mechanistic study mentioned above, selected factor-interaction experiments (e.g., elevated  $\text{CO}_2 \times \text{UV-B}$ ) need to be undertaken. Ideally, some also might be approached at the ecosystem level.

Finally, models developed from a sound empirical base are needed to integrate findings, conduct sensitivity analyses, extrapolate to different weather conditions, species combinations, etc. These will be imperfect to be certain, but as with all aspects of global changes in climate, atmospheric composition and human land use, models are necessary to provide a broader view of our future environment.

These few recommendations are not designed to describe a comprehensive research plan and do not deal with several important issues (potential direct effects on consumers, detritivores or the need to resolve radiation weighting factors described briefly early in this essay). They do, however, describe the underpinnings and direction we feel research in this area must take in order to be ultimately useful for public decision making.

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