LIGHTING CONSIDERATIONS IN CONTROLLED ENVIRONMENTS FOR NONPHOTOSYNTHETIC PLANT RESPONSES TO BLUE AND ULTRAVIOLET RADIATION

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INTRODUCTION

This essay will consider both physical and photobiological aspects of controlled environment lighting in the spectral region beginning in the blue and taken to the normal limit of the solar spectrum in the ultraviolet. The primary emphasis is directed to questions of plant response to sunlight. Measurement and computations used in radiation dosimetry in this part of the spectrum are also briefly treated.

Because of interest in the ozone depletion problem, there has been some activity in plant UV-B research and there are several recent reviews available (Caldwell et al. 1989, Tevini and Teramura 1989, Teramura 1990, Tevini 1993, Caldwell and Flint 1994). Some aspects of growth chamber lighting as it relates to UV-B research were covered earlier (Caldwell and Flint 1990). Apart from work related to the blue/UV-A receptor (Senger 1984), less attention has been given to UV-A responses (Klein 1978, Caldwell 1984).

SOLAR UV AND BLUE RADIATION

The justification and interest in much of the plant research in controlled environments revolve around how plants may respond to solar radiation in nature. This is the emphasis of this essay. Some very different requirements may be in order for research probing the nature of chromophores, etc. However, these requirements can be very specific to particular research efforts and will not be considered.

In sunlight, blue and UV-A (320-400 nm)[1] radiation are tightly coupled and covary with changes in solar angle, atmospheric turbidity and cloudiness (Madronich 1993). The UV-B (280-320nm) is somewhat uncoupled from UV-A and blue light in that it is independently influenced by atmospheric ozone absorption. Even with the same total atmospheric ozone column thickness, as solar angle (and therefore atmospheric pathlength) varies, UV-B is affected to a greater degree than the longer wavelength radiation. Much interest of late has centered on the question of stratospheric ozone reduction and its influence on ground-level UV-B. However, even in the absence of ozone reduction, the normal latitudinal gradient in ozone column thickness and prevailing solar angles result in a much greater latitudinal gradient of UV-B (especially at the

[1]As originally defined (Coblentz, 1932), the UV spectrum is: UV-A 315 to 400 nm, UV-B 280 to 315 nm, and UV-C <280 nm. However, the division between UV-A and UV-B is often taken as 320 nm.

shorter wavelengths) than in UV-A and visible radiation (e.g., Caldwell et al. 1980, Madronich 1993).

Within the UV-B waveband, the spectral distribution is also greatly influenced by changes in atmospheric ozone column thickness and solar angle (Fig. 1).

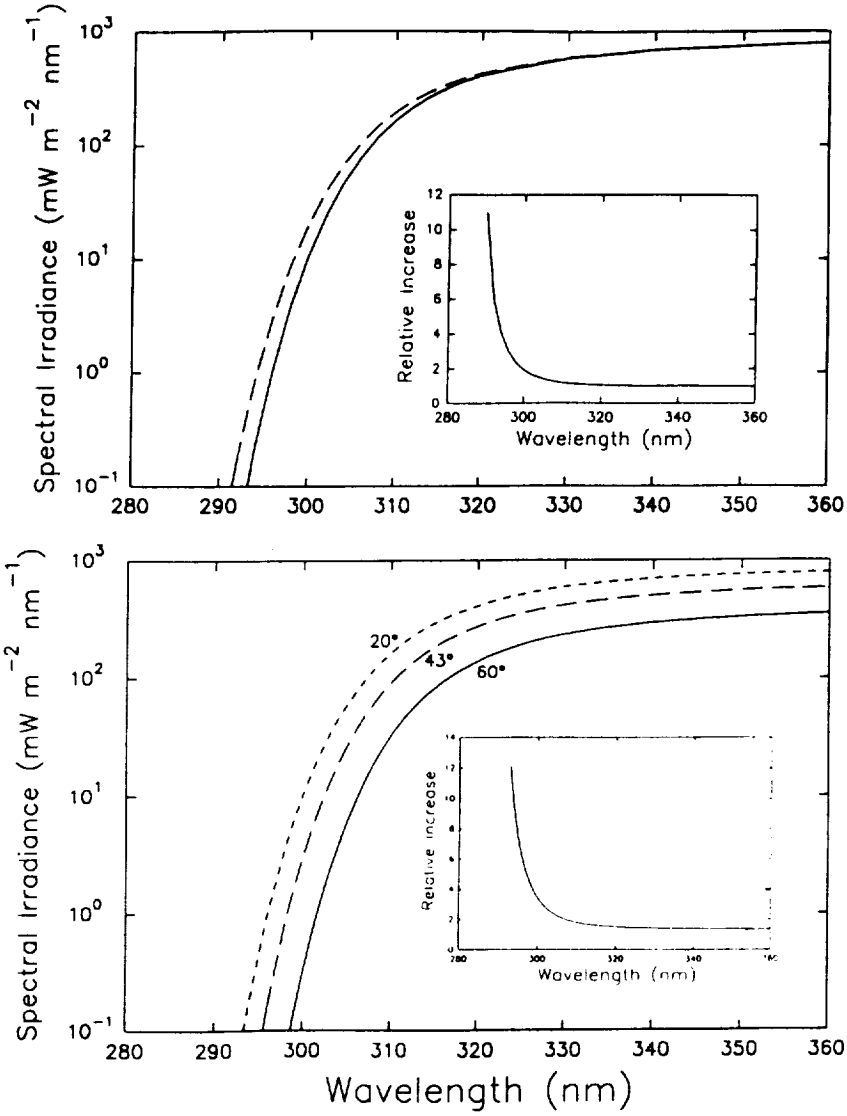

Fig. 1. (upper) Solar spectral irradiance (direct beam + diffuse) at noon at a temperate latitude (40°) location in summer with normal (continuous line) and a 20% reduction of the ozone column (dashed line). In the inset is the factor for relative increase of spectral irradiance at each wavelength due to the ozone column reduction. (lower) Solar spectral irradiance at a temperate latitude (40°) location in summer at different solar angles (20°, 43° and 60° from the zenith). In the inset is the factor for relative increase of spectral irradiance when the solar zenith angle changes from 43° to 20°.

These large alterations of spectral distribution within the UV-B are the result of the absorption cross section (absorption coefficient) of ozone. The abrupt decrease of spectral irradiance as a

function of decreasing wavelength has not, to our knowledge, been satisfactorily achieved without using ozone itself as a filter. [Tevini et al. (1990) have achieved this by using ozone to filter natural sunlight in the field. However, the size of the useable plant experimentation space is very limited.] To mimic the change in spectral flux density during the day in controlled environments (as occurs with solar angle changes) would be technically challenging and very costly -- a cost of dubious value for most research goals. Given the unpractical nature of trying to trying simulate solar spectral irradiance, some compromises are normally taken as will be discussed later.

SOME PHOTOBIOLOGICAL CONSIDERATIONS

Ultraviolet and blue radiation can elicit many photobiological reactions in plants, some of which have been rather well studied (e.g., the blue/UV-A receptor phenomena -- Senger 1984). Other responses are less well understood in terms of chromophores and other photobiological characteristics. Nevertheless, action spectra and/or suspected chromophore absorption spectra are often used conceptually in dosimetry and prescribing requirements for radiation. This is analogous with what has been done in illumination technology and in considering visible radiation for photosynthesis. For example, the standard photopic relative luminous efficiency or "standard eye" curve is used a weighting factor in all photometric units (such as luminous flux, candela or lux). Basically, this involves a dimensionless factor at each wavelength that weights the radiation according to the ability of the human eye to see this wavelength of radiation. When the weighted spectral irradiance is integrated with respect to wavelength, a single value of luminous flux is obtained. This has served well in lighting engineering since light from various sources can be compared with respect to human ability to utilize the light such as in reading. In a similar vein, a standard to represent photosynthetically active radiation has been widely adopted, namely the total photon flux density in the waveband 400-700 nm. The introduction of an integrating dosimeter for total photon flux in this waveband by Biggs et al. (1971) was a very useful contribution for plant scientists. With this "quantum sensor", one can easily measure what is commonly termed "photosynthetically active radiation -- PAR" or "photosynthetic photon flux -- PPF". 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, though appreciable in the blue part of the spectrum, is usually not serious for the types of dosimetry normally conducted. Thus, with relative impunity, the plant scientist can make his/her measurements and be primarily concerned with other aspects of the research.

Analogous approaches have been used in the UV-B and dosimeters have been devised for obtaining a weighted integrated measure of "effective" UV-B -- the weighting function usually is that describing sunburning of human skin (e.g., Berger 1976, Diffey 1986). We are not aware of this approach with dosimeters incorporating biological weighting factors being taken in the UV-A. There are several difficulties with this approach in the spectral region spanning the blue to UV-B -- some which are related to the manner in which solar radiation behaves and some to the many potential chromophores that may be important in this part of the spectrum. This diversity is indicated in Fig. 2.

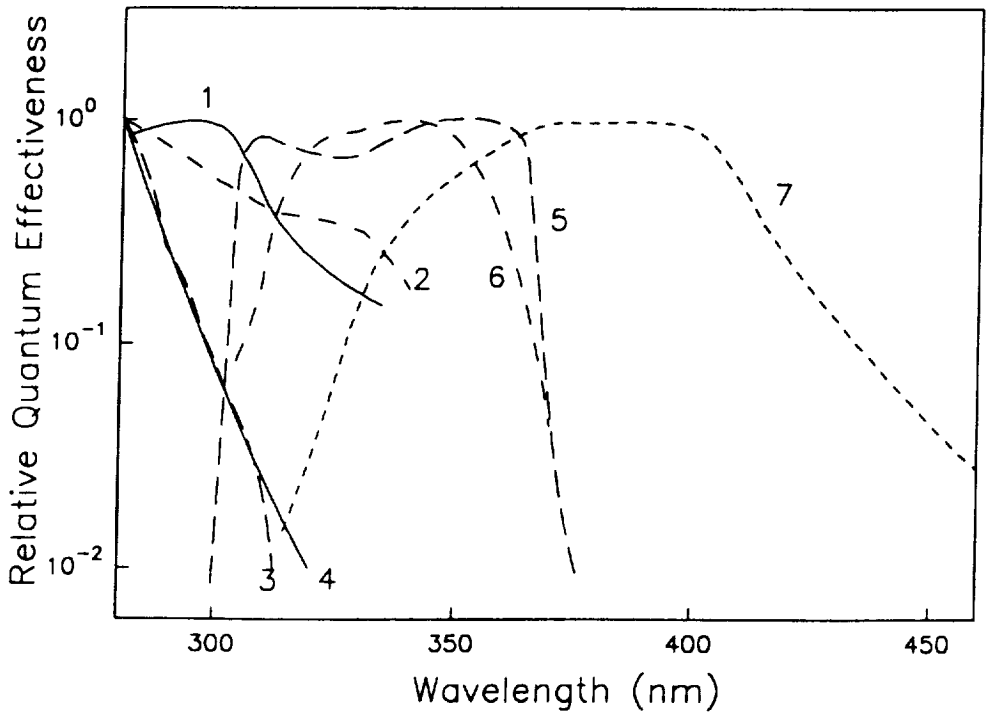

Fig. 2. Action spectra for various plant or microbial photobiological reactions in response to UV-B and UV-A radiation: (1) flavonoid pigment induction in cell cultures of parsley (Wellmann 1983); (2) photosystem II activity inhibition of isolated spinach thylakoids (Bornman et al. 1984); (3) DNA-dimer formation in intact alfalfa seedlings (Quaite et al. 1992); (4) inhibition of net photosynthesis in intact dock (*Rumex patientia*) leaves (Caldwell et al. 1986); (5) growth delay allowing more effective repair of UV damage (called photoprotection) in *E. coli* (Kubitschek and Peak 1980) (6) carotenoid protection of UV damage in *Sarcina lutea* (Webb 1977); (7) photoreactivation of UV damage to DNA (dimer formation) in *E. coli* (Jagger et al. 1969) .

This collection is certainly not comprehensive, but should convey the diverse characteristics of these spectra. Of course, a plant response may involve coaction of two or more chromophores.

In addition to the diversity of chromophores, the nature of solar radiation also complicates representation of plant-effective radiation, especially in the UV-B. In the UV-A and visible spectrum, spectral irradiance does not undergo large changes as a function of wavelength. However, in the UV-B, attenuation by ozone comes into play and spectral irradiance drops by orders of magnitude with decreasing wavelength -- more than 4 orders of magnitude within 25 nm (Fig. 1). When weighting functions (derived from action spectra or suspected chromophore absorption spectra) are applied to the spectral irradiance, small differences in the weighting functions can result in very large differences in the "effective" radiation (Caldwell et al. 1986, Madronich 1993). Thus, a situation quite different from evaluating PPF in the visible spectrum exists. Since simulating the solar spectrum in controlled environments is, for the most part, never achieved, one is forced to compare the "effective" radiation in sunlight with the "effective" radiation derived from the lamp systems no matter how the effective radiation is defined (i.e., which weighting function is employed). This may not always be apparent to the reader of such research reports, but is a necessary component of evaluating the radiation environment of the

plants. Depending on the weighting functions used, large discrepancies can arise. This is discussed in detail elsewhere (Caldwell et al. 1986). In principle, these discrepancies would be much less of problem in the UV-A and blue part of the spectrum. However, there has been little attention to analogous dosimetry at these longer wavelengths.

DOSIMETRY

As mentioned above, a few UV-B dosimeters have been devised. Even if these dosimeters function 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 weighting functions. Alternatively, one can measure the spectral irradiance, wavelength by wavelength. This is certainly the most desirable since the spectral irradiance can be convoluted with any desired weighting function. However, an instrument that can measure satisfactorily in the solar UV-B spectrum involves much more demanding (and expensive) characteristics than is required in the visible spectrum. The primary reason for this is the orders-of-magnitude change in flux in this part of the spectrum (Kostkowski et al. 1982, Diffey 1986). This essay is not an appropriate place for a discussion of spectroradiometer measurements and characteristics, but the reader should at least be warned of the difficulties.

There are also geometrical considerations. Unlike solar visible radiation which is dominated by the direct beam component, the proportion of global solar UV radiation in the diffuse component is much greater and this proportion increases with decreasing wavelength. At the shorter (and generally most biologically effective) UV-B wavelengths, most of the radiation is in the diffuse component. Certainly the geometrical representation of radiation in controlled environments seldom approaches that of solar radiation in nature and it would probably not be a wise investment to attempt this for most problems. Nevertheless, the assumptions made and the geometrical characteristics of the radiation sensors (cosine law adherence, etc.) further complicate the comparison of sunlight with controlled environment lighting.

INTERACTIONS OF DIFFERENT SPECTRAL COMPONENTS

The use of biological weighting functions (whether built into dosimeters or used in computations of effective radiation from spectral irradiance determinations) carries the assumption that the plant response represented by the weighting function also applies with polychromatic radiation. The weighting functions are derived from action spectra (usually obtained with monochromatic radiation) or suspected chromophore absorption spectra (necessarily derived from monochromatic radiation). Whether the aggregated monochromatic radiation responses, i.e., the integral of weighted spectral irradiance, adequately represents responses in polychromatic radiation has seldom been tested. Nevertheless, this is the common assumption.

Some of the action spectra in the UV-A and blue light represented in Figure 2 are specifically for secondary processes that modify primary responses to UV-B -- usually mitigating the damage. Even if all the primary UV-B and secondary UV-A and blue light driven processes were perfectly understood, the question is whether their aggregated responses interact in a simply additive fashion. Or, would synergistic responses occur? A mechanistic understanding of these interactions eludes us thus far. Therefore, one must rely on empirical clues. For example, a few

experiments have been performed to test how visible and UV-A radiation affect UV-B sensitivity.

Experiments specifically designed to investigate the influence of PPF level on UV-B sensitivity showed that UV-B effects were less pronounced if plants were under higher PPF (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 high PPF and UV-A flux had mitigating effects on UV-B reduction of plant growth (Caldwell et al. 1994). However, the mitigating effects of UV-A and PPF did not act in a simple additive manner nor in a fashion that could be predicted from combinations of the action spectra represented in Figure 2. Although they did not specifically test the effect of different levels of UV-A and PPF on UV-B sensitivity, Middleton and Teramura (1993a) showed that UV-A could exert both positive and negative effects on plant growth and some physiological characteristics in a greenhouse study. Fernbach and Mohr (1990) demonstrated coaction of UV-A/blue light receptor and phytochrome and they also showed UV-A to be important in modifying UV-B sensitivity (Fernbach and Mohr 1992).

SPECTRAL BALANCE IN GROWTH CHAMBERS AND GREENHOUSES

The ratio UV-B:UV-A:PPF in sunlight is approximately 1:23:270 when taken on a total photon flux basis in each waveband (without weighting) (Caldwell et al. 1994). This is seldom replicated in controlled environments (Fig. 3).

To provide some perspective on how the average daily UV-B and PPF employed in greenhouse and growth chamber experiments relate to such 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:PPF employed in the experiments. Of these only 14 reported enough information to determine the daily UV-B and PPF used. Since some of 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 PPF and the daily UV-B used. Again because of multiple treatments, ten data points are available. (We feel simply reporting the maximum midday values of PPF in greenhouse experiments does not provide a useful indication of the daily average values.) Even though maximum PPF in growth chambers may not be particularly great, in some experiments with sufficiently long daylengths, the integrated total-day UV-B:PPF ratio was close to that of the natural environment. However, in most of these experiments the UV-B:PPF ratios were far from those experienced by plants in the field.

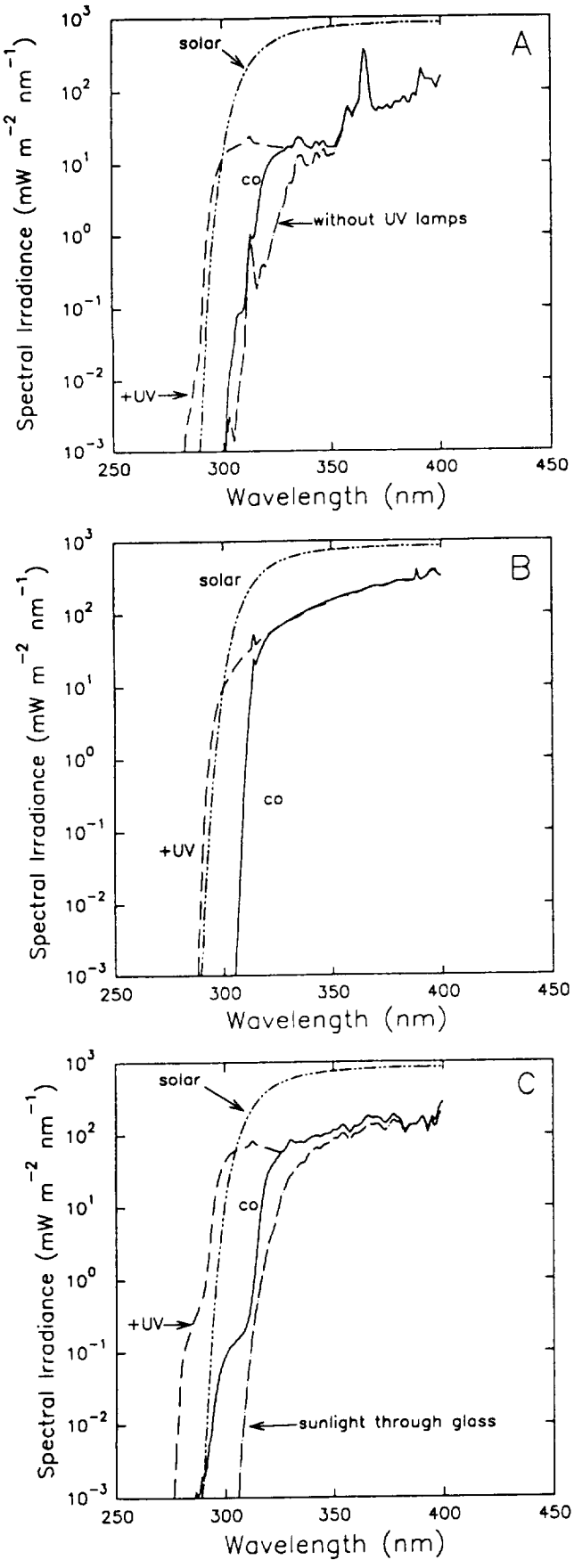

Fig. 3. Spectral irradiance in two types of growth chambers and in a greenhouse where different UV-B experiments were conducted. **A**. A chamber equipped with a combination of metal halide and high pressure sodium lamps combined with the normal filtered UV-B fluorescent lamps used in UV-B plant experiments: (**solar**) solar radiation at noon at midlatitude in the summer; (**+UV**) chamber lighting combined with UV-B fluorescent bulbs filtered with cellulose acetate plastic film; (**co**) the same, but with the UV-B bulbs filtered with polyester film (often used as a control); (**without UV lamps**) the chamber lighting without UV-B bulbs. **B**. A chamber with 6000-W xenon short arc lighting: (**solar**) solar radiation as in A.; (**+UV**) the xenon lamp filtered with cellulose acetate film; (**co**) the xenon lamp filtered with polyester film. **C**. Spectral irradiance in a glasshouse with the filtered UV-B fluorescent bulbs as in A: (**solar**) solar radiation as in A, outside the glasshouse; (**+UV**) UV-B fluorescent lamps filtered by cellulose acetate plastic film with background high pressure sodium lamps and sunlight coming into the glasshouse; (**co**) UV-B bulbs filtered by polyester film with background high pressure sodium lamps and sunlight coming into the glasshouse; (**sunlight through glass**) background winter sunlight coming into the glasshouse without other lamps.

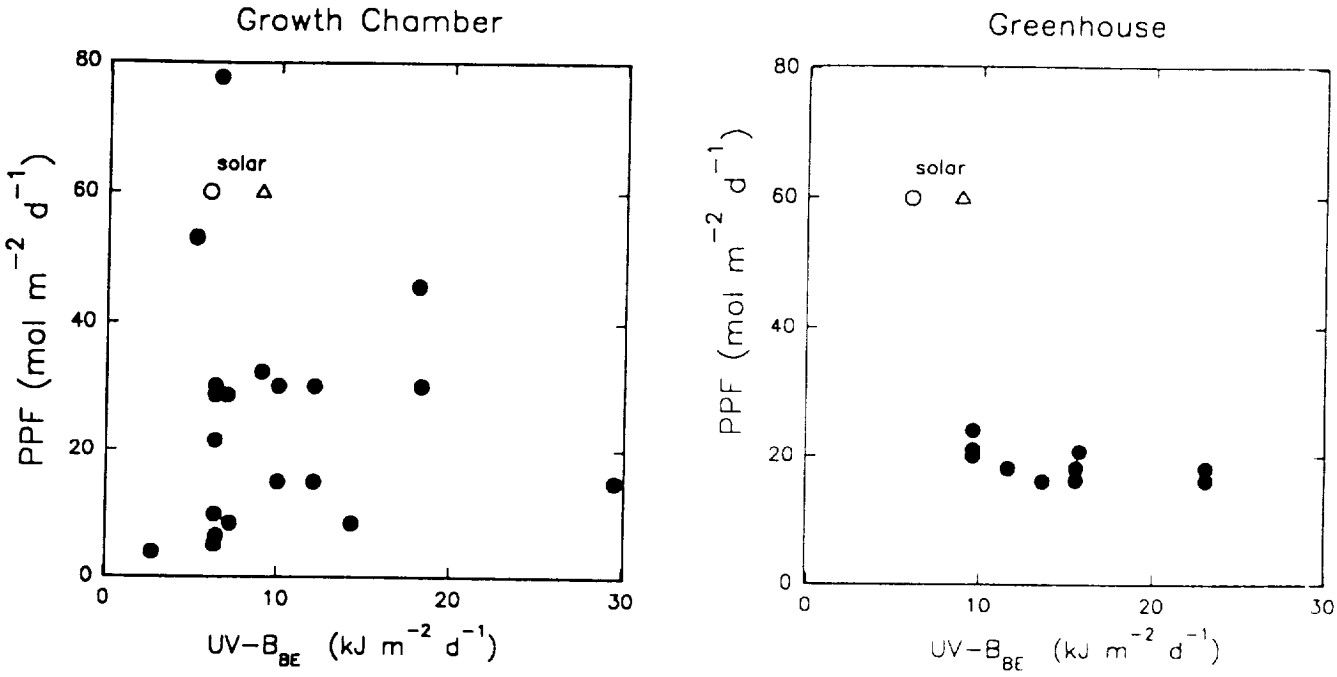

Fig. 4. Average daily integrated biologically effective UV-B using the generalized plant action spectrum weighting function (Caldwell 1971) normalized to 300 nm (UV-B_{BE}) and total photon flux in the 400-700 nm waveband (PPF) employed in growth chamber and greenhouse experiments (●). For comparison, measured solar UV-B_{BE} and PPF on a clear day (3 August 1993) at 1450 m elev. and 41° N latitude (○) and the corresponding value computed (using the measured values as a basis) for a 20% reduction of the ozone column (△). From Caldwell and Flint (in press).

Usually the UV-A is not reported in greenhouse and growth chamber experiments. However, since a portion 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 (Fig. 3), fluxes of UV-A comparable to those in sunlight are not generally anticipated (Middleton and Teramura 1993b). The levels of UV-B and PPF 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. However, if the research interest does not relate to UV-B effects, but rather specific responses to UV-A or blue light, different criteria should be considered and the UV-B:UV-A:PPF ratio may be of less interest.

CONCLUSIONS AND COMPROMISES

It would be quite desirable to replicate the solar radiation, both in flux density and spectral distribution, in controlled experiments. Assumptions regarding appropriate weighting functions,

etc. would be obviated and a greater realism in experiments could be realized. However, duplicating the sun with artificial lighting, especially in the UV-B, is not presently attainable and may only be realized in the future with inordinate expense. A less ideal, but more practical, solution will usually be a compromise. For example, rather than trying to achieve the perfect spectral shape of sunlight, a more achievable goal would be to maintain the ratio of UV-B:UV-A:PPF similar to that in solar radiation. Increased duration of irradiation in growth chambers may have to compensate for not achieving peak midday solar flux densities. Of course, the degree to which different compromises are acceptable depends on the particular research interests. In any case, investment of resources and time in good dosimetry is of prime importance. Most lamps and many types of filters undergo ageing and lamp output is often temperature dependent. Thus, frequent measurements need to be conducted. In greenhouse environments, the solar radiation background continually changes while supplemental lamps in use may change relatively less. Thus, rather than simply representing peak values or midday averages, irradiation in different spectral bands should be reported in mean daily integrals. Use of weighting functions can seldom be avoided, at least for work in the UV-B. However, it is important to appreciate the assumptions and limitations involved in their use.

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