

IS UV-B A HAZARD TO SOYBEAN PHOTOSYNTHESIS AND YIELD? RESULTS OF AN OZONE-UV-B INTERACTION STUDY AND MODEL PREDICTIONS

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ABSTRACT

Current levels of tropospheric ozone suppress photosynthesis and yield in soybean. Also, it has been suggested that increased ground-level UV-B as a result of stratospheric ozone depletion may have additional deleterious effects. A three-year field study, conducted in open-top chambers, was undertaken to uncover possible interactions between these putative stressors. Ozone treatments resulted in the expected and well-documented reductions in photosynthesis, yield and acceleration of senescence. However, UV-B treatments not only failed to induce any significant interactions, but did not induce any significant reductions in photosynthesis or yield, even at levels simulating a 35% column ozone depletion. Reconciliation of our data with other predictions of physiological dysfunction and crop losses due to increased UV-B was attempted by examining the models used to predict ground-level UV-B, ground truthing, and critically reviewing the literature. Comparison of ground-based measurements at our location with the Green et al. (9) model, frequently used to predict ground-level UV-B, showed consistent over-predictions of clear-sky UV-B of 32% on an annual basis. We believe that similar over-predictions have led some researchers to underestimate the actual dosages used, with the result that the effects reported would normally only occur at much higher UV-B levels and are much greater than would occur at the reported dosages. Lack of ground-level UV-B monitoring in many experiments has obscured and perpetuated this problem. Also, there generally has been no adjustment of enhancement levels for either season or weather conditions, except where modulated systems have been used, so that effects are additionally exaggerated for these reasons. Interpretation of experimental results is confounded by these four factors (model over-prediction, seasonal changes, weather changes, and failure to monitor UV-B) and made much more difficult when UV-B enhancement experiments are conducted under greenhouse growth conditions. Additional illustrative calculations for greenhouse conditions are included for consideration. Examination of the literature in light of these findings indicates there is little evidence that increased ground-level UV-B, well in excess of current predictions for the next century, will pose any hazard to soybean growth and productivity.

INTRODUCTION

Recently Stolarski et al. [17] demonstrated statistically significant downward trends in stratospheric ozone over much of the northern hemisphere. The year-round trend was estimated as -1.8% per decade and, although much higher (-2.7%) in the winter, the

trends were about -1.0 to -1.3% per decade over most of the crop-growing season at mid-northern latitudes. As a result of these decreases there is a potential for increased ultraviolet-B (UV-B) radiation (280-320nm) at ground level which may pose a hazard to natural aquatic and terrestrial ecosystems as well as suppress

worldwide crop production. On the other hand, tropospheric O₃ currently is recognized as the single most phytotoxic regional air pollutant and already may be responsible for a 15% decrease in production of some crops [10]. It is important to determine if increased UV-B and tropospheric O₃ acting in combination pose an additional threat to the normal development and yield of crops. Therefore, the objective of the experiments reported here was to determine what, if any, interactions might occur between pollutant ozone and UV-B with regard to photosynthesis and yield and to determine their extent and identify their cause.

Soybean was chosen because it is the most extensively studied of the crop plants in terms of UV-B response in field situations and we also have a large data base on the response of this species to tropospheric ozone. For this experiment we used three soybean cultivars. One of the cultivars (Essex) has been reported to be susceptible to UV-B damage [12,21] and was found to be normally sensitive to ozone damage.

MATERIALS AND METHODS

Although details of the materials and methods for this experiment can be found in Miller et al. [13], salient features of that study for the 1990 season will be repeated here for the convenience of the reader.

Three soybean cultivars [*Glycine max* (L.) Merr. cvs. Essex, Coker 6955, and S 53-34] were grown in 151 pots in a 2:1:1 (by volume) mixture of soil, sand, and Metro-Mix 220 (W.R. Grace Co., Cambridge, MA)^a in open-top field chambers at Raleigh, NC, USA. Plants were watered daily and fertilized biweekly with "Peters Blossom Booster" (10-30-20 N-P-K) (Grace-Sierra Horticultural Products Co., Milpitas, CA)^a and three times during the season with "Peters STEM" soluble trace elements and micronutrient mix (Grace-Sierra Horticultural Products Co., Milpitas, CA).^a Ozone treatments of charcoal-filtered air (CF) and ozone additions to a final concentration of 1.7x ambient were administered over a 132-d period starting at germination and continuing to harvest. The seasonal mean of the 12-h daily mean [O₃] in the CF and supplemental O₃ treatments were 24 and 83 nL L⁻¹, respectively.

Low, medium, and high UV-B supplements were provided by banks of fluorescent lamps (model UVB-313, Q-Panel Co., Cleveland, OH)^a suspended in the

open-top chambers as previously described. Lamps in the low treatment were wrapped in polyester film to filter out radiation less than 315 nm; therefore, this treatment also served as the control for UV-A (320-400nm) and visible radiation emitted from the lamps. Lamp irradiance in the medium and high UV-B treatments was filtered with cellulose diacetate (0.13 mm thickness) to remove radiation below 290 nm. Lamp banks were kept at a constant height of 0.4 m above the canopy, and the irradiance was varied by fluorescent dimmer controls on the lamp ballasts.

Broadband erythral meters (model 2D, Solar Light Co., Philadelphia, PA)^a with a spectral response very similar to that of the Robertson-Berger (R-B) meter were used to set the lamp bank irradiance levels each day and a Robertson-Berger meter was used to monitor solar UV continuously. Ambient and chamber irradiances were also measured with a UV-visible spectroradiometer (model 742, Optronics Laboratories, Inc., Orlando, FL)^a equipped with a 3.7-m-long quartz fiber optics cable and Teflon diffuser head. The spectroradiometer was calibrated with an NIST-traceable 200W tungsten-halogen lamp standard of spectral irradiance (model 220A, Optronics Laboratories, Inc., Orlando, FL)^a driven by a current regulated power source (model 65, Optronics Laboratories, Inc., Orlando, FL).^a Wavelength calibration was checked periodically by comparison with Hg emission lines from a UVB-313 lamp. The broadband erythral meters were calibrated against the spectroradiometer as previously described [1], and biologically effective UV-B irradiance (UV-B_{BE}) was calculated by applying Caldwell's generalized plant action spectrum [5], normalized to 300 nm (PAS300), to the spectroradiometer scans. In 1992 an additional broadband erythral instrument (Model UVB-1 UV Pyranometer; Yankee Environmental Systems, Montague, MA)^a was used for monitoring solar UV-B.

Stratospheric ozone losses corresponding to the supplemental UV-B_{BE} radiation levels were calculated from the radiative transfer model derived from Green [9] by Björn and Murphy [3]. The model was extensively modified^b for ease of use and flexibility, and additional functions were added for PAS300

^aMention of a company or product does not imply an endorsement by the United States Department of Agriculture.

weighting and the Robertson-Berger meter spectral sensitivity curve. Inputs and outputs of the model were confirmed by ground-based measurements. The model predicted a total daily UV-B_{BE} irradiance for 21 June of 5.45 kJ m⁻² with an aerosol coefficient = 1. In 1990 an average daily solar UV-B_{BE} of 4.88 ± 0.12 (s.d.) kJ m⁻² measured by the Robertson-Berger meter for the 30 d surrounding 21 June indicated acceptable agreement with the model. Also on 21 June, the daily supplemental UV-B_{BE} irradiance in the three treatments was set to 0, 4.43, and 8.13 kJ m⁻² for the low (control), medium, and high UV-B treatments. Due to an average UV-B shading effect of the open-top chambers of 24%, the total daily UV-B_{BE} irradiance for the three treatments was 4.14, 8.57, and 12.27 kJ m⁻². The treatments thus corresponded to an increase in the O₃ column thickness of 15% and decreases of 20%, and 35% respectively.

Supplemental UV-B treatments were administered as a constant daily addition with the lamp output levels being set each day, from sowing to harvest, while the ozone was being dispensed. To compensate for seasonal changes in photoperiod and solar UV-B irradiance, the supplemental irradiance levels were adjusted biweekly; thus, relatively constant ozone column depletion simulations were maintained [1]. For example, on 1 September the solar clear sky irradiance was calculated as 4.66 kJ m⁻². On that basis, the lamps in the high UV treatment would be set to deliver an additional 5.27 kJ m⁻² for a total exposure of 9.93 kJ m⁻², still corresponding to a column ozone depletion of 35% even though there was 19% less UV-B_{BE} delivered to the plants than on 21 June. At season's end, the actual exposure figures were refined according to the ground-based measurements provided by the R-B meter. Over the entire 1990 experimental period, therefore, the mean daily UV-B_{BE} irradiances were 3.02, 6.24 and 8.98 kJ m⁻². On overcast days the treatments were discontinued if the UV-B_{BE} irradiance fell below 20% of the maximum calculated for the Raleigh, NC, location on 21 June for more than 30 minutes. Solar UV-B_{BE} was evalu-

ated every 2 h afterward, and treatments were resumed if the overcast cleared.

Net carbon exchange rate (NCER), leaf conductance, and transpiration were made with an LI-6000 portable photosynthesis system (Li-Cor, Inc, Lincoln, NE)^a and chlorophyll fluorescence induction was measured at room temperature using a pulse amplitude modulated chlorophyll fluorometer (PAM-101-103, H. Walz, Effeltrich, Germany)^a. The efficiency of excitation energy capture by open PSII reaction centers in dark-adapted leaves was determined by F_v/F_m , where $F_v = F_m - F_o$ [11]. The photochemical fluorescence-quenching coefficients (q_p) were determined as described by Horton [11].

The Ozone/UV-B interaction portion of the study was conducted for two years (1989 and 1990), while the UV-B portion was continued for a third year (1991). UV-B enhancement details for 1990 are given above while the details for all three years may be found in Miller *et al.* [13].

All parameters were compared by analysis of variance and differences deemed not significant if $P > 0.05$. Further statistical details are also in Miller *et al.* [13].

RESULTS AND DISCUSSION

The UV-B_{BE} enhancement treatments for 1990 are shown in Figure 1. The data points and lines are the total measured and calculated doses at the plant canopy level and are the sum of solar and supplemental UV-B_{BE}. Seasonal means for 1989 and 1991 are available in Miller *et al.* [13].

Detailed analysis of the growth, photosynthesis, and yield of these experiments [13] shows the expected declines as well as the accelerated senescence of the plants typical of ozone exposure. Miller *et al.* [13] could find no UV-B effects on net carbon exchange rate (NCER), stomatal conductance, or transpiration in Essex soybean, and so the UV-B treatments were combined for further analysis. To illustrate the lack of UV-B effect on photosynthesis, we present the NCER data broken down into UV-B treatments in Figure 2. Clearly the ozone treatments accelerated the decline from peak photosynthetic competence without any discernable significant or lasting effects or interactions of the UV-B treatments. Similar segregation of data by ozone, but not UV-B, was apparent in other parameters as well. In particular

^a Copies of the executable code which will run in MS-DOS without an interpreter or compiler may be obtained on request from the senior author. The programs are available on a single 3.5" DD or HD diskette, a single HD 5.25" diskette or two DD 5.25" diskettes. If possible, a return mailer and blank diskettes should accompany the request.

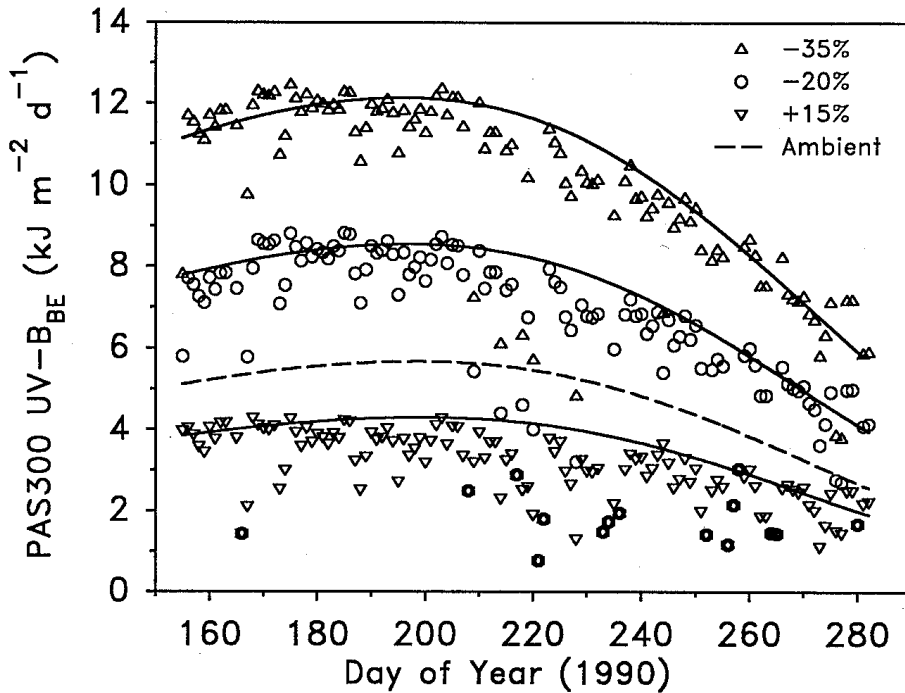


Figure 1. UV-B treatment levels for the 1990 experiment. Lines were calculated from Björn and Murphy (1985). Numbers on figure indicate the simulated column ozone change in the different treatments. Ambient UV-B_{BE} data are not shown to reduce clutter.

there was no UV-B suppression of growth or yield for any of the three cultivars used for any of the three years of the study. In addition, in 1991 analysis failed to show any UV-B effects on the variable component of chlorophyll fluorescence induction or q_p at either 26 or 69 days after planting (Table 1). There was, however, a statistically significant increase in NCER during the period of 69-71 days after planting. The reasons for this difference are not clear; however, it is difficult to attach much physiological significance to such small differences. Other studies failed to find any UV-B effects on peroxidase activity or chlorophyll levels [2]. The only UV-B effect apparently consistent with many other studies was the increase in UV absorbance of leaf extracts indicative of increased production of flavonoids and other phenolic compounds.

Given the current apparent perception that crops

are at risk [22,24] from increased UV-B radiation, it is important to reconcile our results with those from other laboratories. Comparisons between laboratories, especially for field and greenhouse studies, are not trivial exercises since reporting of growth conditions, UV-B dose, and dose monitoring is frequently confusing. Therefore, the remainder of this paper will be devoted to a discussion of dosing procedures and calculations, which we believe have lead to large underestimates of actual UV-B treatment levels and consequent large overestimates of potential UV-B effects.

There are four reasons why UV-B dosages could be underestimated:

- 1) use of a radiative transfer model that overestimates ground level UV-B in certain circumstances;
- 2) lack of daily monitoring of ambient ground level UV-B during the course of an experiment;

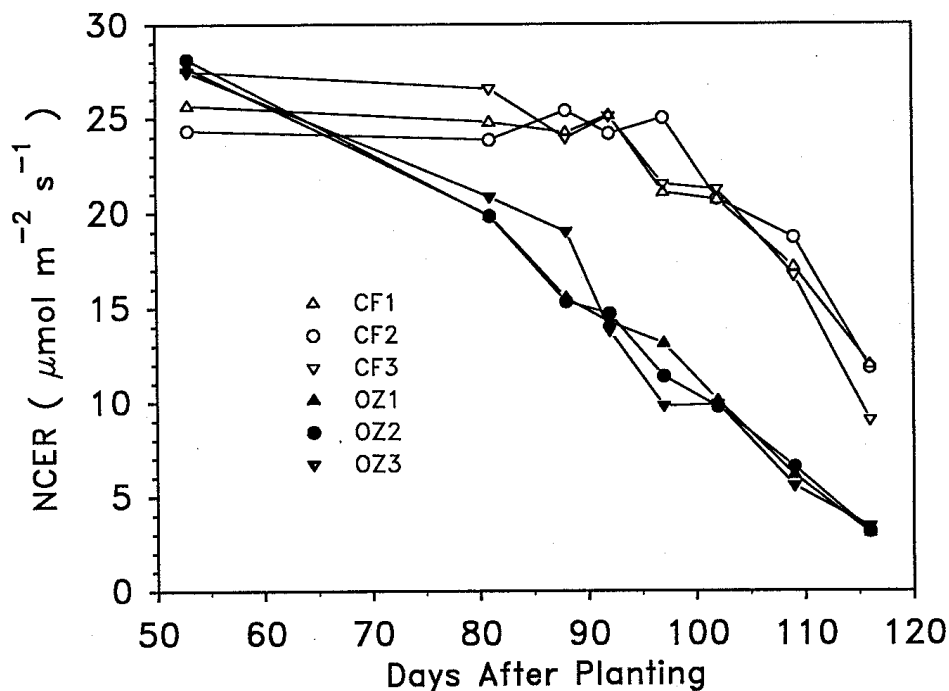


Figure 2. Net carbon exchange rate for the 1990 experiment.

3) lack of treatment level adjustments according to weather conditions; and

4) lack of treatment level adjustments to account for seasonal changes.

In addition there has been infrequent reporting of daily photosynthetically active radiation (PAR). These factors are not completely independent of each other so that inadequate monitoring of ground-level UV-B can worsen and perpetuate the errors based on a poor model prediction. Daily PAR values also will be related to weather and season. To illustrate the difficulties posed by these four factors, we shall use data from our field site at Raleigh, NC, USA for 1992. The measurements and model predictions will require only small adjustments to apply generally to mid-latitudes (30-40°N) and low elevations in the eastern United States. Before proceeding, however, we stipulate, for purposes of discussion later in this paper, our

acceptance that as a worst case scenario the current year-round trend of stratospheric ozone depletion of 1.8% per decade [17] will apply to the normal cropping seasons and continue unchanged for the next 100 years.

It is well established that UV-B damage to plants is aggravated by low levels of PAR [6,14,19,23,25]. However, methods of reporting PAR during experiments tend to be cursory and difficult to interpret in relation to UV-B experiments. Although reporting daily midday PAR maxima during the experiment can give a general impression of weather conditions, we feel it would be far preferable to report actual daily integral data throughout the experiment as well as the daily UV-B_{BE} integrals and perhaps the ratio of these two.

Figure 3 clearly illustrates the frequency of days at our location when PAR is below its clear sky value.

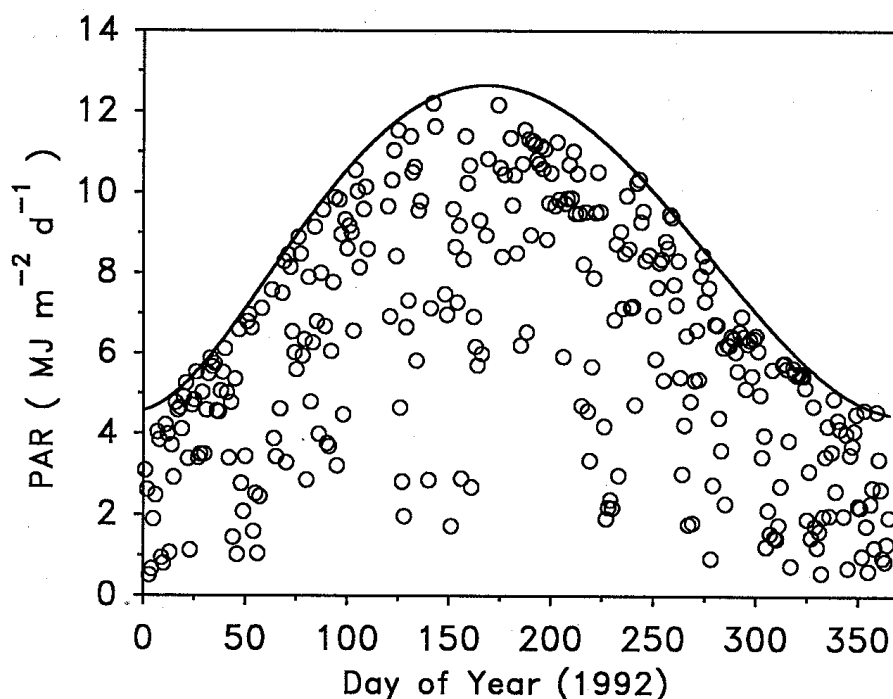


Figure 3. Photosynthetically active radiation falling on a horizontal sensor in 1992. The boundary line shown is an arbitrary function used only for estimating maximum PAR values through the year and is not based on an analytical model.

Analysis of these data indicates that over the entire year, mean PAR averaged only 69% of maximum. Figure 4 illustrates the same point for PAS300 UV-B_{BE} for which the annual mean was only 70% of the clear sky maximum. Also shown in Figure 4 is the excellent agreement between ground-based measurements and the data boundary line calculated from the Björn and Murphy [3] model that we have used throughout these studies.

Further analysis of the data in these two figures shows that the minimum annual ratio of clear sky PAR/UV-B_{BE} (units of each are $J m^{-2} d^{-1}$) is about 1700 and falls to 1150 for a 20% column ozone depletion. Further, the average ratio for days 100 to 300, which under ambient conditions is normally 2250, would be 1490 for a 20% reduction of the ozone column. This ratio varied cyclically throughout the year and rose to an annual maximum of about 7800 during the winter months. It seems only prudent to

maintain realistic ratios of PAR and UV-B_{BE} radiation during enhancement experiments to ensure that capacity for photorepair is adequate and that other physiological processes affected by PAR and UV-B are in a natural balance as well as to stimulate synthesis of UV screening compounds [4,14,15].

The choice of radiative transfer model to use is also a matter of great importance as can be seen from Figures 4 and 5. As mentioned earlier, the Björn and Murphy [3] model adequately describes the envelope of ambient UV-B measurements made at our field site throughout the year when ozone column data from the Nimbus 7 Total Ozone Mapping Spectrometer (TOMS) is used as input (Figure 4). By itself, the model will calculate an ozone column but the algorithm tends to overestimate the average column thickness except for about a two month period in the fall (Figure 5). It would appear from Figure 4 that, even with TOMS inputs, the model overestimates the UV-

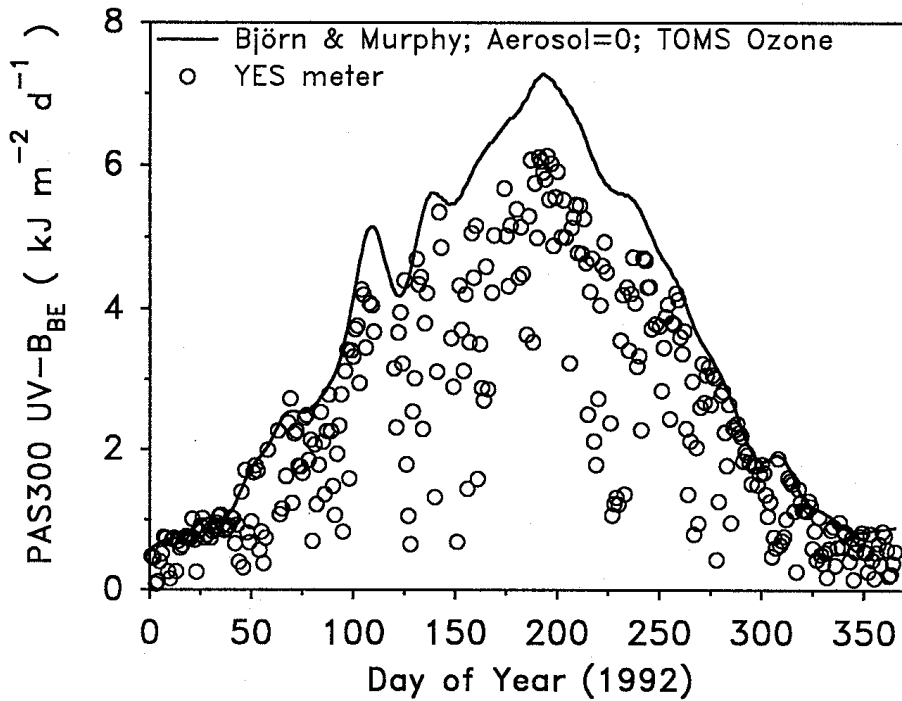


Figure 4. Comparison of ground-based measurements with a YES erythral sensing instrument. The erythral data were converted to PAS300 units by using the ratio PAS300/Erythral irradiance determined from the Björn and Murphy (1985) model for each day of the year. The line was calculated from the model with the following Inputs: atmospheric pressure = 1000 mb; relative humidity = 0.5; aerosol coefficient = 0; environment = rural green farmland; TOMS ozone; and location = 35.75°N, 78.67°W.

B_{BE} in the mid-summer period. That discrepancy can be explained by remembering that the boundary line describes clear sky conditions and the actual summertime radiation is more often attenuated by aerosols, spotty clouds, and haze than it is in winter. Inclusion of an arbitrary annual aerosol function, which rises from 0 in the winter to a maximum of 2 in mid-summer along a cosine curve, drops the boundary peak in Figure 4 onto the top of the data.

In the past, the Green *et al.* [7,8] model was used to calculate ground-level UV- B_{BE} for the purpose of setting supplemental levels. In Figure 5 we compare the output from both the Green *et al.* [8] and the later Björn and Murphy [3] models. Clearly evident in this figure is that the Green *et al.* model overestimates UV- B_{BE} at the ground by a substantial amount throughout

the year whether a mean annual value for the ozone column or daily TOMS data are used. When TOMS data are used for both models, the Green *et al.* model overestimates UV- B_{BE} by an average, over the year, of 32% when compared to the Björn and Murphy model. Therefore, supplements calculated from the Green *et al.* model will be understated in terms of column ozone depletion. A supplement calculated to simulate a 20% reduction in column ozone by the Green *et al.* model will actually deliver radiation consistent with a 25% reduction under the best (clear sky) circumstances (Table 1). It is important to note that this 5% discrepancy in column ozone represents a 25% calculational error and a 38% difference in the level of the UV- B_{BE} supplement delivered to the canopy.

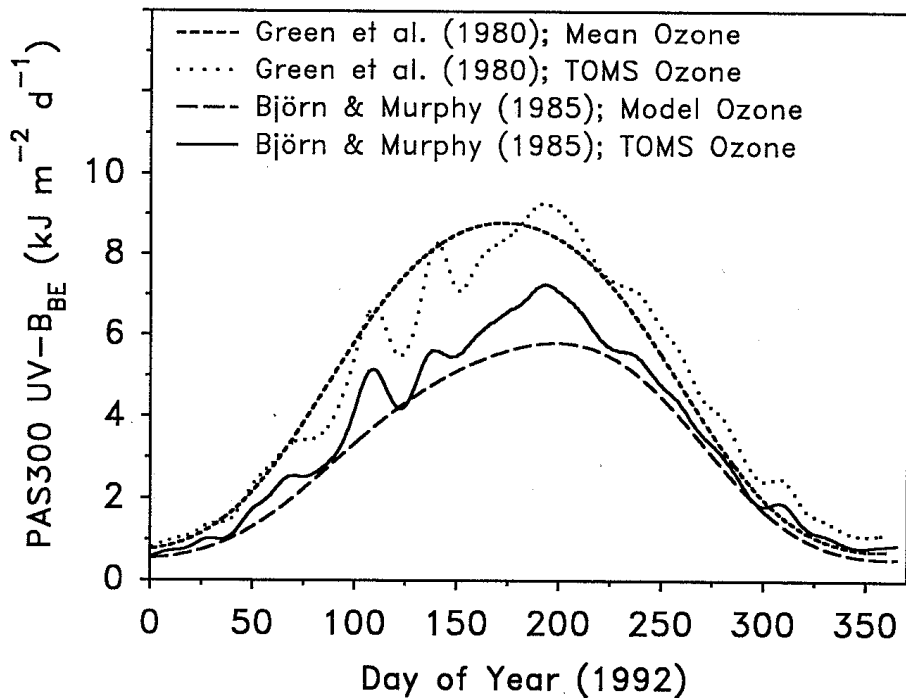


Figure 5. Comparison of the Green et al. (1980) and the Björn and Murphy (1985) models, both with and without TOMS data. Inputs for both models were the same as for Figure 4. Additional inputs for the Green et al. model are elevation = 114m and for the curve not using TOMS data, an annual average of 0.315 cm atm was entered. In the absence of TOMS data, the Björn and Murphy model generates its own column ozone data, shown as the long dashed line.

Calculations presented in Table 2 show how poor model estimates are compounded by not adjusting for clouds or aerosols. These calculations are based on Figure 3 and the assumption that, when PAR is reduced by clouds or other reasons, $UV-B_{BE}$ is also attenuated by the same fraction. While this assumption is probably not exact for any particular day, earlier calculations in this paper show that it is very close on an average basis. That is, while average PAR is 69% of the envelope value, average $UV-B_{BE}$ was 70% of the envelope. In any case, the assumption will satisfy the purpose of illustrating the problems of not adjusting supplements according to weather.

Earlier we showed that a Green et al. (8) supplement designed to simulate a 20% ozone column reduction actually simulated a 25% reduction under

clear sky conditions. Now, if PAR only falls 10% (to 90% of PAR_{MAX}), as happens on 3 out of every 4 days, that same supplement represents a 27% depletion if calculated as follows: ambient $UV-B_{BE}$ was discounted for clouds by the same fraction as PAR; the ozone column necessary (OCN) to deliver that discounted level under clear skies was calculated; the fixed supplement was added to the reduced ambient value to obtain the total dose (TD); and, finally, the reduction in OCN necessary to pass the TD was calculated. Thus, although the TD seen at canopy height is less under cloudy conditions, the ratio of $PAR/UV-B_{BE}$ is decreased dramatically.

On an average day, with 69% of PAR_{MAX} , the calculated supplement actually represents a 30% ozone depletion. On as many as one day in four that

Table 1. Chlorophyll fluorescence ratios of leaf disks and NCER of soybean leaves treated from emergence to maturity with three levels of supplemental UV-B radiation. Values are means \pm se; n=18; **P<0.01.

Treatment	Days after Planting	F_v/F_m	q_p	NCER ($\text{mol m}^{-2} \text{s}^{-1}$)
Control	26	0.83 ± 0.01	0.71 ± 0.3	-
Medium UV-B	26	0.83 ± 0.01	0.71 ± 0.3	-
High UV-B	26	0.83 ± 0.01	0.67 ± 0.3	-
Control	69-71	0.85 ± 0.01	0.74 ± 0.01	21.1 ± 0.3
Medium UV-B	69-71	0.85 ± 0.01	0.72 ± 0.02	$22.7 \pm 0.2^{**}$
High UV-B	69-71	0.86 ± 0.01	0.72 ± 0.01	$23.1 \pm 0.3^{**}$

Table 2. Influence of cloud cover and model-based overestimates of ground-level UV-B_{BE} on a simulated 20% ozone column depletion for Raleigh, NC, 1992. The supplement necessary to simulate the depletion was calculated for clear skies for the summer solstice using the Green *et al.* (1980) model and an aerosol coefficient=0. The effects of cloud cover were estimated assuming that UV-B_{BE} is reduced by the same fraction as PAR for any particular day and then the model-based error was added. For the greenhouse, a "control" level of $8.5 \text{ kJ m}^{-2} \text{ d}^{-1}$ and a 20% depletion level of $12.5 \text{ kJ m}^{-2} \text{ d}^{-1}$ were calculated from Green *et al.* (1980). Actual depletions given here are based on the Björn and Murphy (1985) model. PAR/UV-B_{BE} was calculated only for the field simulation using $\text{PAR}_{\text{MAX}} = 12.6 \text{ MJ m}^{-2} \text{ d}^{-1}$. The actual normal ratio would be 1950, dropping to 1480 for a 20% ozone reduction.

(PAR/PAR _{MAX}) 100 <	% of Total Days	Compound Simulated Ozone Depletion			
		Field	PAR/UV-B _{BE}	Greenhouse control	Greenhouse -20%
100 %	-	25	1313	20	36
90 %	76	27	1258	24	40
75 %	48	29	1153	31	45
69 % (Annual Mean)	41	30	1106	33	47
50 %	25	35	927	42	54
25 %	10	44	584	56	65

same supplement represents a 35% depletion, and every 10 days the canopy can be expected to experience UV-B_{BE} consistent with a 44% reduction in column ozone. Thus, in the field, treatment levels designed to approximate the worst case for ozone depletion over the next century will, on every fourth day, deliver radiation consistent with depletions of very nearly twice that level. In addition, PAR is reduced and the plants are presumably even more susceptible to UV-B damage.

In the greenhouse the choice of model and adjustments for weather become even more important since greenhouse glass does not normally transmit UV-B and the entire dose must be supplied by artificial means. Thus, if a clear-sky UV-B_{BE} of $8.5 \text{ kJ m}^{-2} \text{ d}^{-1}$ is calculated, as from the Green *et al.* [8] model, and the entire "ambient" level is supplied by lamp banks, then under clear-sky conditions this "control" level already represents a 20% column ozone reduction. Making additional corrections for average cloud cover

Table 3. Soybean yield responses to supplemental PAS300 UV-B_{BE}. Target simulations and supplements were taken from the papers. Clear sky simulations were calculated from Björn and Murphy with aerosol coefficient = 0 and the compound average simulations are discounted for aerosols and cloud cover as in Table 1. Yield changes are indicated as either increases (+), decreases (-) or no change (nc) if P>0.05. Notations in the yield change column identify putative sensitive (S) and resistant (R) cultivars. A ? indicates cultivars that have not been studied enough to classify.

Source	Green et al. Simulation Target (%Depletion)	Supplement (kJ m ⁻² d ⁻¹)	Normal (kJ m ⁻² d ⁻¹)	Clear sky simulation (% Depletion)	Compound average simulation (% Depletion)	# CVYs	Yield Change
Teramura & Murali (1986)	16	4.5	5.6	28	34	6	1 - (York) 5 nc (1S, 4?)
Teramura et al. (1990)	16	3	5.6	22	30	12	5+ (2S, 3R) 2 - (1S, 1R) 5 nc (3S, 2R)
Sinclair et al. (1990)	16	3	7.0	18	22	6	6 nc (1R, 5?)
Miller et al. (1993)	-	2.35	5.6	-	22 ¹	7	7 nc (3S, 4?)
Teramura et al. (1990)	25	5.1	5.6	30	36	10	1+ (1R) 5 - (4S, 1R) 4 nc (1S, 3R)
Sullivan & Teramura (1990)	25	5.1	5.6	30	36	2	2 nc (2S)
Miller et al. (1993)	-	4.81	5.6	-	36 ¹	7	7 nc (3S, 4?)

1. Based on ground measurements throughout the season.

means on an average day this same 8.5 kJ m⁻² d⁻¹ represents a 33% ozone depletion. Taking this illustration one step farther, we can calculate the supplement necessary to simulate a 20% ozone depletion by the Green et al. model (+4 kJ m⁻² d⁻¹). By supplying the total daily dose from lamp banks, we calculate from Björn and Murphy [3] that the dose really simulates a 36% ozone depletion for clear-sky conditions and a 47% reduction for an average day. Strictly speaking, the values in Table 2 apply only to the summer solstice; thus the actual dosages may be even higher at different times of the year.

Having established the magnitude of possible

dose reporting errors, we would like to examine previous yield studies within that context. In the experiments at Raleigh presented by Miller et al. [13], the irradiance levels were estimated by model prior to the experiments, but the reported dosages were calculated after conclusion of the experiment from actual ground measurements as shown in Figure 1. Adequate information, however, is not available for other studies on soybean [16,18,20,21].] On the basis of the Björn and Murphy model and assuming similar cloud cover and aerosol figures as our location at Raleigh, we can estimate some corrections to their reported dosages that can be used as a basis for

comparison. In addition, we shall examine the available field data on the basis of cultivar-years (CVYs), wherein one CVY represents yield data from one cultivar collected during a single season. Thus 2 CVYs would represent the same cultivar tested during two years or for one year within different experiments or locations. On this basis, then, we can break down the available data as in Table 3.

There are a total of 50 CVYs included in Table 2 where "normal" values for PAS300 UV-B_{BE} were calculated using Björn and Murphy P3] with an aerosol coefficient of 0. Where available in the literature, the target levels of ozone column depletion, generally calculated using the Green *et al.* [8] model, also are listed. Supplement levels were taken as given in the appropriate papers except for Teramura and Murali [20] where the supplement was calculated from the given total daily dose. The clear-sky simulations in Table 3 were calculated from Björn and Murphy [3] based on the sum of the normal daily flux and the supplement. The dosages then were discounted for likely cloud cover and aerosols to arrive at an estimate of the average dosages applied to the plants. In the case of Miller *et al.* [13] the values presented are based on actual ground measurements during the season. It also should be noted that Miller *et al.* [13] adjusted the treatment levels for seasonal changes. Since such adjustments were not performed in the other studies, the actual compound average simulations would be even somewhat higher than presented here.

Examination of the compound average simulation values reveals that actual treatment levels in two of the 16% target depletions were probably as high as twice the stated levels based on the Green *et al.* [8] model, while the third exceeded its target by an additional 6% depletion. The end result is that actual treatments were clustered into two groups, one representing a 22% ozone depletion and the other a 30 to 36% depletion level. These groups are approximately equal to and about twice the worst case scenario for ozone depletion for the next century. There are only 13 CVYs included in the 22% category, and none showed any statistically significant change in yield as a result of UV-B treatment. Of the remaining 37 CVYs, 6 (16%) showed yield increases, 8 (22%) yield decreases, and 23 (62%) no change at all. Looking at all 50 CVYs collectively, regardless of treatment level, we can see that 72% showed no change, 12% increased yield, and 16% decreased yield as a result of

UV-B treatments. Perhaps even more revealing is to consider the case of the putative sensitive cultivar Essex, identified as the sensitive (S) in Table 2, which comprises 40% of the CVYs reported here. Surprisingly, this "sensitive" cultivar exhibited yield decreases in only 25% of the years tested, and none at the 22% ozone depletion level. The rest of the time Essex yield increased or remained unchanged in response to UV-B treatment.

A somewhat more liberal approach might be to examine the data on the basis of the clear-sky simulations. In this case the data may be segregated into treatments of <30% ozone depletion levels and 30% depletion, which puts 31 CVYs in the former category and 19 in the latter. For an ozone depletion level <30%, only 10% of the CVYs showed yield decreases while the remaining 90% either increased or did not change. The sensitive cultivar Essex showed a yield decrease in only 1 out of 10 CVYs at this level of treatment and a yield increase in 2 of those 10 CVYs. Of the 19 CVYs included in the 30% category of treatment, yield declined in 5 CVYs, remained the same in 13 and increased in 1.

The data in Table 2 can be summarized as follows: at treatment levels approximating the worst case scenario for the next century, there is very little evidence to suggest that UV-B threatens soybean yields and at treatment levels 1.5 to 2 times that level, the data indicate decreased yields only about 25% of the time in a sensitive cultivar.

CONCLUSIONS

We have attempted to reconcile the results of our experiments with the popular notion that increased UV-B radiation may have a major effect on soybean production. Examination of the literature from this perspective shows that reported UV-B doses are frequently underestimated. In part, these differences may arise from the use of the Green *et al.* [8] predictive model that consistently overestimates ground-level UV-B. Calculated supplements therefore also are overestimated for a target ozone column depletion. In addition, cloud cover, atmospheric aerosols, and seasonal differences further contribute to the under-estimation of actual doses.

In the light of these findings, it appears that increases in ground-level UV-B, well in excess of current projections for the next century, will not

constitute any direct hazard to soybean production.

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REFERENCES

- Booker, F.L., E.L. Fiscus, R.B. Philbeck, A.S. Heagle, J.E. Miller, and W.W. Heck. 1992a. A supplemental ultraviolet-B radiation system for open-top field chambers. *J. Environ. Qual.* 21:56-61.
- Booker, F.L., J.E. Miller, and E.L. Fiscus. 1992b. Effects of ozone and Uv-B radiation on pigments, biomass and peroxidase activity in soybean. *In* R.L. Berglund (ed.), *Tropospheric Ozone and the Environment: Effects, Modeling and Control II*. Air and Waste Management Association, Pittsburgh, PA. p. 489-503.
- Björn, L.O., and T.M. Murphy. 1985. Computer calculation of solar ultraviolet radiation at ground level. *Physiol. vegetal* 23:555-561.
- Bruns, B., K. Hahlbrock, and E. Schafer. 1986. Fluence dependence of the ultraviolet-light-induced accumulation of chalcone synthase mRNA and effects of blue and far-red light in cultured parsley cells. *Planta* 169:393-398.
- Caldwell, M.M. 1971. Solar ultraviolet radiation and the growth and development of higher plants. *In* A.C. Giese (ed.), *Photophysiology*. Academic Press, New York. pp.131-177.
- Cen, Y-P., and J.F. Bornman. 1990. The response of bean plants to UV-B radiation under different irradiances of background visible light. *J. Exp. Bot.* 41:1489-1495.
- Green, A.E.S., T. Sawada, and E.P. Shettle. 1974. The middle ultraviolet reaching the ground. *Photochem. Photobiol.* 19:251-259.
- Green, A.E.S., K.R. Cross, and L.A. Smith. 1980. Improved analytical characterization of ultraviolet skylight. *Photochem. Photobiol.* 31:59-65.
- Green, A.E.S. 1983. The penetration of ultraviolet radiation to the ground. *Phys. Plant.* 58:351-359.
- Heck, W.W. 1989. Assessment of crop losses from air pollutants in the United States. *In* J.J. Mackenzie and M.T. El-Ashry (eds.), *Air Pollution's Toll on Forests and Crops*. Yale University Press, New Haven. pp.235-315.
- Horton, P., and J.R. Bowyer. 1990. Chlorophyll fluorescence transients. *In* J.L. Harwood and J.R. Bowyer (eds.), *Methods in Plant Biochemistry: Lipids, Membranes, and Aspects of Photobiology*. Academic Press, London. pp.259-296.
- Krizek, D.T. 1981. Plant physiology: Ultraviolet radiation. *In* S.B. Parker (ed.), *1981 Yearbook of Science and Technology*. McGraw-Hill, New York. pp.306-309.
- Miller, J.E., F.L. Booker, E.L. Fiscus, A.S. Heagle, W.A. Pursley, S.F. Vozzo, and W.W. Heck. 1993. Effects of ultraviolet-B radiation and ozone on growth, yield, and photosynthesis of soybean. *J. Environ. Qual.* in press.
- Mirecki, R.M., and A.H. Teramura. 1984. Effects of ultraviolet-B irradiance on soybean V: The dependence of plant sensitivity on the photosynthetic photon flux density during and after leaf expansion. *Plant Physiol.* 74:475-780.
- Ohl, S., K. Hahlbrock, and E. Schäfer. 1989. A stable blue-light-derived signal modulates ultraviolet-light-induced activation of the chalcone-synthase gene in cultured parsley cells. *Planta* 177:228-236.
- Sinclair, T.R., O. N'Diaye, and R.H. Badges. 1990. Growth and yield of field-grown soybean in response to enhanced exposure to ultraviolet-B radiation. *J. Environ. Qual.* 19:478-481.
- Stolarski, R., R. Bojkov, L. Bishop, C. Zerefos, J. Staehelin, and J. Zawodny. 1992. Measured trends in stratospheric ozone. *Science* 256:342-349.
- Sullivan, J.H., and A.H. Teramura. 1990. Field study of the interaction between ultraviolet-B radiation and drought on photosynthesis and growth in soybean. *Plant Physiol.* 92:141-146.
- Teramura, A.H. 1980. Effects of ultraviolet-B irradiances on soybean I: Importance of photosynthetically active radiation in evaluating ultraviolet-B irradiance effects on soybean and wheat growth. *Physiol. Plant.* 48:333-339.
- Teramura, A.H., and N.S. Murali. 1986. Intraspe-

- cific differences in growth and yield of soybean exposed to ultraviolet-B radiation under greenhouse and field conditions. *Environ. and Exptl. Bot.* 26:89-95
21. Teramura, A.H., J.H. Sullivan, and J. Lydon. 1990. Effects of UV-B radiation on soybean yield and seed quality: A 6-year field study. *Physiol Plant* 80:5-11.
 22. Teramura, A.H., and J.H. Sullivan. 1991. Potential impacts of increased solar UV-B on global plant productivity. *In* E. Riklis (ed.), *Photobiology*. Plenum Press, New York. pp.625-633.
 23. Teramura, A.H., R.H. Badges, and S.V. Kossuth. 1980. Effects of ultraviolet-B irradiances on soybean II: Interaction between ultraviolet-B and photosynthetically active radiation on net photosynthesis, dark respiration, and transpiration. *Plant Physiol.* 65:483-488.
 24. Tevini, M., and A.H. Teramura. 1989. UV-B effects on terrestrial plants. *Photochem. Photobiol.* 50:479-487.
 25. Warner, C.W., and M.M. Caldwell. 1983. Influence of photon flux density in the 400-700nm waveband on inhibition of photosynthesis by UV-B (280-320nm) irradiation in soybean leaves: Separation of indirect and immediate effects. *Photochem. Photobiol.* 38:341-346.