

Field Study of the Interaction between Solar Ultraviolet-B Radiation and Drought on Photosynthesis and Growth in Soybean¹

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ABSTRACT

Soybean, *Glycine max* (L.) Merr. cv Essex, plants were grown in the field in a 2 × 2 factorial design, under ambient and supplemental levels of ultraviolet-B (UV-B) radiation (supplemental daily dose of 5.1 effective kilojoules per square meter) and were either well-watered or subjected to drought. Soil water potentials were reduced to −2.0 megapascals by the exclusion of natural precipitation in the drought plots and were maintained at approximately −0.5 megapascal by supplemental irrigation in well-watered plots. Plant growth and gas exchange characteristics were affected under both drought and supplemental UV-B radiation. Whole-leaf gas exchange analysis indicated that stomatal limitations on photosynthesis were only significantly affected by the combination of UV-B radiation and drought but substrate (ribulose biphosphate) regeneration limitations were observed under either stress. The combined effect of both drought and UV-B radiation on photosynthetic gas exchange was a reduction in apparent quantum efficiency and the rapid appearance of biochemical limitations to photosynthesis concomitant with reduced diffusional limitations. However, the combination of stresses did not result in additive effects on total plant growth or seed yield compared to reductions under either stress independently.

Reductions in global stratospheric ozone column thickness of 1.7 to 3.0% from 1969 to 1986 have recently been reported with seasonal reductions of up to 50% over the Antarctic (21). Such reductions are projected to result in increased solar UV-B² radiation reaching the earth's surface. UV-B radiation has been shown to reduce plant biomass, leaf area, and photosynthetic capacity in soybean (*Glycine max* [L.] Merr.), and its

¹ This work was supported in part by the U.S. Environmental Protection Agency's Environmental Research Laboratory in Corvallis, OR (CR 812 150-02-0), Scientific Article No. 8044, Contribution No. A-4997 of the Maryland Agricultural Experiment Station. Although the work described in this article was funded in part by the U.S. Environmental Protection Agency, it has not been subjected to the agency's peer and policy review. It therefore does not necessarily reflect the views of the agency and no official endorsement should be inferred.

² Abbreviations: UV-B, ultraviolet radiation between 290 and 320 nm; RuBP, ribulose 1,5-bisphosphate; UV-B_{BE}, biologically effective ultraviolet-B radiation; *A*, CO₂ assimilation; *E*, transpiration; *g_s*, stomatal conductance; *C_i*, internal CO₂ concentration; AQE, apparent quantum efficiency; CEC, cation exchange capacity.

effectiveness may be modified by other environmental factors (20). For example, sensitivity to UV-B radiation is influenced by growing conditions such as low PPFD (18), mineral deficiency (19), and water stress (20). Multiple simultaneous stresses, such as increases in solar UV-B radiation and drought, could lead to additive, compensatory or other synergistic effects on plant physiology and crop yield. Therefore, it is important to evaluate the interaction between solar UV-B radiation and some other key environmental stresses in crop plants in order to predict future effects on crop yield and productivity.

Water stress is one of the most common stresses plants experience in the field, and an extensive body of literature has been accumulated on the effects of drought on plant productivity and physiology. Some information already exists on the combined effects of UV-B radiation and water stress. Murali and Teramura (20) reported a masking of UV-B radiation effects in drought-stressed soybean and attributed this to anatomical (leaf thickening) and biochemical (flavonoid production) changes induced by drought stress. However, other studies have observed deleterious effects of UV-B radiation in the presence of leaf thickening and elevated flavonoid concentrations (18, 24, 26). Thus alternative explanations should also be considered. Since similar symptoms such as altered growth, morphological changes, or pigment induction may be produced by numerous stresses, it is difficult to explain stress interactions on the basis of symptoms alone. Instead, an increased understanding of the physiological bases of individual stresses may lead to a better explanation of their interactions.

Both drought and UV-B radiation may independently affect photosynthesis, but it is unknown whether they alter photosynthesis by affecting different processes. Ultraviolet-B radiation has been shown to reduce photosynthesis by direct alterations of photosystem II (14), while its effects on stomatal conductance is minimal (20, 22). Drought may reduce photosynthesis by both stomatal closure and biochemical effects (3, 6). Therefore the specific limitations on photosynthesis may vary in response to these specific stresses. Photosynthetic limitations may be evaluated by gas exchange analyses including the functional responses of photosynthesis to light, internal CO₂ concentrations, and O₂ sensitivity (13, 23). Quantitative alterations of these responses indicate whether photosynthesis is limited by diffusional or biochemical processes such as carboxylating enzyme activity, substrate (RuBP) regeneration, or triose phosphate utilization (23). To date, these

limitations have not been evaluated in this manner under enhanced UV-B radiation.

The purpose of this study was to evaluate the interactions between chronic drought stress and UV-B radiation enhancement on field grown soybean and to examine the effects of these stresses on the biochemical and diffusional limitations of photosynthesis.

MATERIALS AND METHODS

Field experiments were conducted from May to October 1986, at the Agricultural Research Center, USDA, Beltsville, MD on a silt loam soil (classification: mesic Aquic Unifluvents; properties: pH 6.6, CEC 4.8 meq 100 g⁻¹, organic matter 0.6%). Soybean, *Glycine max* (L.) Merr. cv Essex, were sown in late May in rows spaced 0.4 m apart at a seeding density of 33 seeds m⁻¹ in four plots of 4.5 m × 2.5 m each. One week after germination, plants were thinned for uniformity in growth to 15 m⁻¹. Natural precipitation was excluded from two of the plots, beginning after planting, by covering them with polyethylene tents just prior to any major precipitation event. Tents were removed immediately after each storm. Soil water potential was maintained at approximately -2.0 MPa in water-stressed plots and at -0.5 MPa in well-watered plots by supplemental irrigation.

Soil water potential and temperature at a depth of 0.25 m were monitored using calibrated Wescor PCT-55-15 soil psychrometers and a Wescor HR-33T dew point microvoltmeter. Six psychrometers were regularly spaced along the central rows of plants in each plot which were used for analysis.

Supplemental UV-B radiation was provided as a 2-step square wave function by filtered Westinghouse FS-40 sunlamps following the procedure outlined in Lydon *et al.* (17). Lamps were suspended above and perpendicular to the planted rows (rows oriented in an east-west direction to minimize shading) and filtered with either presolarized 0.13 mm thick cellulose diacetate (transmission down to 290 nm) for supplemental UV-B radiation or 0.13 mm polyester plastic films (absorbs all radiation below 320 nm) as a control. The spectral irradiance from the lamps was determined with an Optronic Laboratories Inc. model 742 Spectroradiometer, equipped with a dual holographic grating modified to maintain constant temperature by the addition of Peltier heat exchange units, and interfaced with a Hewlett Packard model

85 printing calculator. The spectral irradiance was weighted with the generalized plant response action spectrum (8) and normalized at 300 nm to obtain UV-B_{BE}. Plants under polyester-filtered lamps received only ambient levels of UV-B radiation (8.5 kJ m⁻² UV-B_{BE} during clear sky conditions on the summer solstice calculated according to an empirically derived model (12). Plants beneath the cellulose acetate filters received ambient plus supplemental levels of UV-B. The lamp height above the plants was adjusted weekly to maintain a distance of 75 cm between the lamps and the top of the plants. These heights and an irradiation time of 6 h, centered at solar noon, provided a total UV irradiance approximating that which would be received at Beltsville, MD (39°N) with an anticipated 25% stratospheric ozone reduction during a cloudless day on the summer solstice (13.6 kJ m⁻² UV-B_{BE}) according to an empirical model of Green *et al.* (12).

Since the sensitivity of soybean to UV-B radiation was shown to be the greatest during the transition between vegetative and reproductive growth (27), physiological measurements were conducted during the R-1 to R-2 growth stages, about 8 weeks after planting (11). Net photosynthetic CO₂ assimilation (*A*) and transpiration (*E*) were measured in the field on the central leaflet of attached, fully expanded trifoliolate leaves at the seventh node in temperature-controlled cuvettes. Leaf temperature was measured by a finewire copper-constantan thermocouple and cuvette temperature was maintained by Peltier heat exchange units mounted on the underside of the cuvettes. A small fan inside the cuvette provided mixing and minimized boundary layer conductances. Due to absorption by the cuvette cover there was no solar UV-B radiation in the cuvette so the gas exchange responses represented a cumulative rather than an instantaneous UV-B radiation effect. The influx of CO₂ was measured in an open system using an Anarad AR-600R infrared gas analyzer at a leaf temperature of 28°C and a leaf-air vapor pressure deficit of 1.0 to 1.5 kPa. Transpiration and water vapor *g_s* were calculated from the flux of H₂O vapor into and out of the cuvette. This was measured with an EG&G model 911 and a General Eastern System 1100DP condensation dew point hygrometer. Net photosynthetic CO₂ assimilation, *C_i*, *g_s*, and *E* were calculated according to the equations of von Caemmerer and Farquhar (29). Leaf water potential was determined

Table I. Vegetative Growth and Seed Yield Measurements in Control and UV-B Irradiated Soybeans Grown Under Two Water Regimes

Each value is the mean of 20 plants for vegetative growth and 50 plants for seed yield ± 1 SE. Means in each column followed by the same letter are not significantly different at *P* < 0.05 according to Student Newman-Keuls multiple range test.

Suppl. UV-B dose	Plant Height	Plant Dry Wt	Leaf Area	No. of Pods	SLW ^a	Seed No.	Seed Yield
<i>kJ m⁻²</i>	<i>cm</i>	<i>g</i>	<i>m⁻²</i>		<i>g m⁻²</i>		<i>g</i>
Well-watered							
0	76.9 ± 2.2a	29.0 ± 4.1a	0.14 ± .02a	53.3 ± 4.3a	62.0 ± 2.3a	103.5 ± 5.6a	10.3 ± .52a
5.1	73.5 ± 4.5a	19.0 ± 1.8b	0.09 ± .008b	41.3 ± 2.8b	63.3 ± 3.0a	96.9 ± 5.3a	9.7 ± .49a
Drought-stressed							
0	60.4 ± 3.5b	10.1 ± 1.5c	0.05 ± .01b	27.0 ± 5.4b	68.2 ± 9.3a	44.5 ± 5.8b	3.8 ± 5.3b
5.1	51.7 ± 1.7b	12.9 ± 1.2c	0.06 ± .008b	32.2 ± 3.4b	67.4 ± 2.4a	33.3 ± 5.7b	3.2 ± 5.1b

^a Specific leaf weight.

Table II. Gas Exchange Parameters of Control and UV-B Irradiated Soybeans Grown Under Two Water Regimes

Each value is the mean of three replicates \pm 1 SE. Means in each column followed by the same letter are not significantly different at $P < 0.05$ according to Student Newman-Keuls multiple range test.

Suppl. UV-B dose	A (Ca = 350)	A (Ci = 340)	g_s	E	AQE	Light Saturation (90% A_{max})	Carboxylation Efficiency
$KJ m^{-2}$	$\mu mol m^{-2} s^{-1}$	$\mu mol m^{-2} s^{-1}$	$mmol m^{-2} s^{-1}$		$\mu mol CO_2 \mu mol PPFD^{-1}$	$\mu mol m^{-2} s^{-1}$	$\mu mol CO_2 \mu L C_i^{-1}$
Well-watered							
0	32 \pm 1.8a	37 \pm 1.8a	499 \pm 34a	5.0 \pm .2a	0.069 \pm 0.01a	1435 \pm 69a	0.266 \pm 0.02a
5.1	27 \pm 1.8b	30 \pm 2.0b	439 \pm 39ab	4.6 \pm .2ab	0.055 \pm 0.01ab	1179 \pm 83b	0.190 \pm 0.01a
Drought-stressed							
0	20 \pm 0.6c	23 \pm 1.2c	289 \pm 25b	3.2 \pm .3c	0.060 \pm 0.01a	710 \pm 23c	0.198 \pm 0.02a
5.1	22 \pm 1.7c	24 \pm 1.8c	327 \pm 35b	3.7 \pm .3bc	0.042 \pm 0.01b	981 \pm 46b	0.217 \pm 0.01a

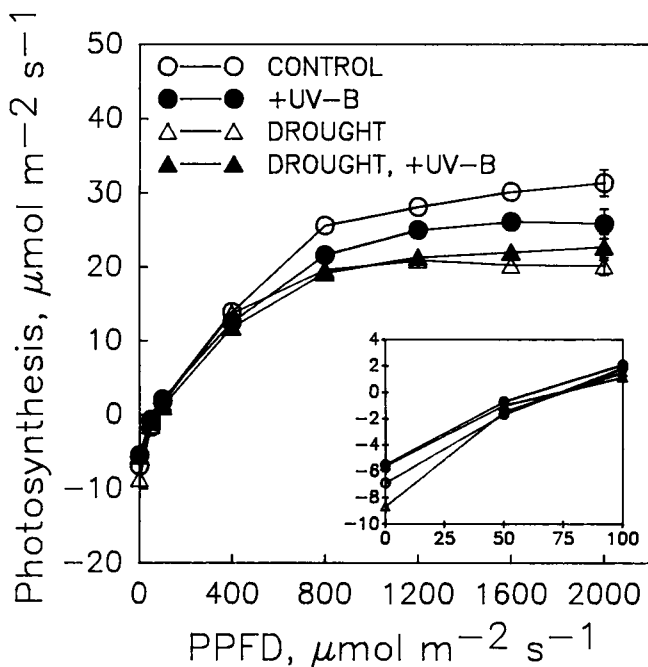


Figure 1. Photosynthetic response to PPFD between 0 and 2000 $\mu mol m^{-2} s^{-1}$ for soybean grown under well-watered conditions with no supplemental UV-B radiation, well-watered with supplemental UV-B radiation, droughted with no supplemental UV-B radiation, and droughted with supplemental UV-B radiation. Symbols represent means for three leaflets and error bars represent maximum standard errors for the curves.

following gas exchange measurements with a PMS Company model 1000 pressure chamber.

The response of A to C_i and incident PPFD were determined on three replicate leaves each. Supplemental lighting was provided as needed with 300 W Westinghouse 56/2 WFL low temperature, PAR floodlamps. Light responses were determined by measuring assimilation at a CO_2 concentration of 340 to 360 and a PPFD of 2000 $\mu mol m^{-2} s^{-1}$ and sequentially decreasing irradiances, by means of a variable transformer to 1600, 1200, 800, 400, 100, 50, and 0 $\mu mol m^{-2} s^{-1}$, as measured with a Li-Cor model 190S quantum sensor. The transformer produced a slight shift in spectral energy distribution only at a PPFD of 50 $\mu mol m^{-2} s^{-1}$ (JH

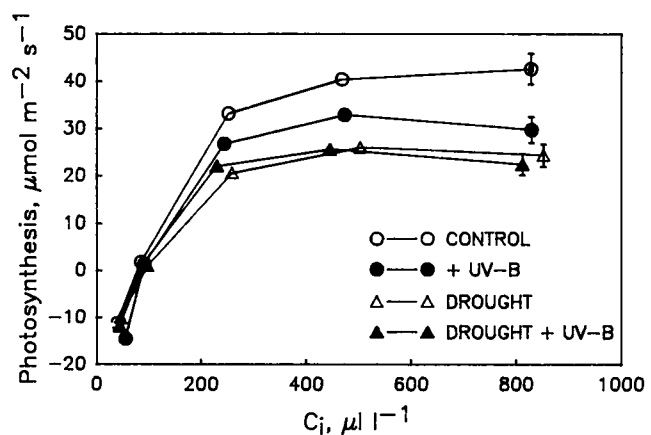


Figure 2. Photosynthetic response to internal CO_2 partial pressures (C_i) for soybean grown under well-watered conditions with no supplemental UV-B radiation, well-watered with supplemental UV-B radiation, droughted with no supplemental UV-B radiation, and droughted with supplemental UV-B radiation. Symbols represent means for three leaflets and error bars represent maximum standard errors for the curves.

Sullivan, GA Carter, unpublished data). Carbon dioxide responses at saturating PPFD were determined by changing ambient CO_2 concentrations in the cuvette. Gas exchange rates were examined at external CO_2 concentrations of approximately 100, 350, 600, and 1000 $\mu L L^{-1}$. The stomatal limitation on photosynthesis was calculated as the percent decrease between A at a C_i of 350 $\mu L L^{-1}$ and at the operational C_i recorded at an ambient CO_2 concentration of 350 $\mu L L^{-1}$ as in Farquhar and Sharkey (10) and alternatively using the simplified path-dependent method of Jones (15) for comparison.

Twenty plants per treatment were harvested (aboveground only) during the full pod (R-4) stage (11) for vegetative growth analysis and the remainder harvested from the treatment rows at maturity for yield analysis. Plant height and the number of leaves, seed pods, and seeds were counted for each plant, and leaf area was determined with a Li-Cor LI-3100 area meter. Plant material was then oven-dried at 60°C for 1 week and weighed.

Data were analyzed by a two-way analysis of variance which tested main effects of UV-B radiation and drought and their

Table III. A Comparison of the Stomatal and Nonstomatal Components of the Limitations on *A* in Soybean when Grown Under UV-B Radiation, Drought, and Both Stresses

The analyses were made according to the calculation of Farquhar and Sharkey (10) and also according to the path-dependent method of Jones (15) assuming either a 'stomata first' or a 'mesophyll first' path.

Treatment	Farquhar and Sharkey Calculation	Jones Calculation			
		Stomata first		Mesophyll first	
		Stomatal	Nonstomatal	Stomatal	Nonstomatal
		%			
Control	13.3				
+ UV-B	11.3	54	46	9	91
+ Drought	13.8	41	59	4	96
+ UV-B and drought	6.2 ^a	67	33	7	93

^a Denotes statistically different from control ($P > 0.05$).

interaction. Significantly different means were separated using the Student Newman-Keuls multiple range test (25).

RESULTS

Soybean growth and yield was generally reduced by drought (Table I), but the effects of supplemental UV-B radiation varied between watering treatments. In well-watered treatments, plant dry weight, leaf area, and number of seed pods were reduced under supplemental UV-B radiation while plant height, specific leaf weight, seed yield, and number were unaffected (Table I). Under drought-stress conditions, supplemental UV-B radiation had no statistically significant effects on plant growth or yield.

Light-saturated photosynthetic rates (at operational and $350 \mu\text{L L}^{-1} C_i$), g_s , and E were reduced by drought stress, whereas photosynthesis was reduced by UV-B radiation only under well-watered conditions and g_s and E were unaffected by UV-B radiation (Table II). AQE between 50 and $100 \mu\text{mol m}^{-2} \text{s}^{-1}$ was reduced by UV-B radiation in the drought-stressed plants but was not significantly affected by UV-B radiation in the well-watered plants (Table II; Fig. 1). The irradiance required to saturate *A* was reduced compared to the well-watered polyester controls by both drought and UV-B radiation but no additive effects were observed. By contrast, light saturation of *A* required a higher PPFD in the plants receiving the combination of stresses compared to drought alone (Table II).

No differences were observed in the apparent carboxylation efficiency (initial slope of the *A-C_i* response), but statistically significant differences appeared at C_i exceeding $200 \mu\text{L L}^{-1}$ (Fig. 2). As C_i neared and reached saturation, *A* was reduced by both drought and UV-B radiation, but no further reductions occurred under the combination of stresses (*i.e.* UV-B radiation had little effect on droughted plants). The stomatal limitations on *A*, when calculated according to Farquhar and Sharkey (10), were reduced only in the combination of stresses (Table III). A comparison of the diffusional contribution of limitations on *A* calculated by the methods of Farquhar and Sharkey (10) and Jones (15) revealed a contrast in terms of partitioning of limitations (Table III). Using the Jones (15) 'path-dependent' method, the stomatal contribution toward photosynthetic limitation increased under the combination

of stresses when calculated using the stomata-first calculation. However, when the mesophyll-first path was considered, the stomatal limitation was minimal in all cases.

DISCUSSION

Drought reduced growth and photosynthesis in soybean, but no additional reductions in plant growth were exhibited when plants also received enhanced UV-B radiation. However, UV-B radiation under well-watered conditions reduced photosynthetic capacity, plant dry weight, leaf area, and number of pods. Masking of UV-B radiation effects in the presence of drought may be due in part to anatomical (leaf thickening) or biochemical (pigment accumulation) adjustments to drought which ostensibly also protect plants from UV-B radiation through screening mechanisms (20). However, other factors potentially limiting UV-B effectiveness in drought-stressed plants could occur at the physiological level. For example, it has been observed that drought may reduce plant phosphorus levels (16), and phosphorus deficiency has been shown to reduce the sensitivity of soybean to UV-B radiation (19). Also drought may delay cell division, in part through reduced cell elongation, which may play a role in the initiation of cell division (5). Since UV-B radiation directly affects cell division, a general growth delay has been recognized as one means of protection from UV-B radiation (2). Therefore, the effectiveness of UV-B radiation may be reduced in the presence of drought or other stresses which result in growth delay or concurrent increases in UV-B protective mechanisms.

In addition to general growth reductions, both drought and UV-B radiation reduced the photosynthetic capacity of soybean and altered the apparent limitations to assimilation. Stomatal limitations on photosynthesis may be reduced under drought or other stress conditions (10); although, in this study, when they were calculated in a conventional manner (10), these limitations were only reduced under the combination of stresses. This may imply that some synergistic effects increased the biochemical limitations present; however, a simple calculation of the stomatal limitation does not allow the calculation of the magnitude of other limitations (4). We sought to partition diffusional and non-diffusional limitations by using the path-dependent methodology of Jones (15) and found a contrasting importance for the stomatal limitation

depending on which method of calculation was employed. In an assessment of the limitations imposed by spectral changes in visible light, Assman (1) also observed contrasting importance of stomatal limitations. In the present study, where stomatal conductance was only minimally affected by UV-B radiation, it seems likely that the mesophyll-first path would be more appropriate, and if this were the case then the results of the two methods of calculation (10, 15) yielded similar results. In drought, where significant reductions in stomatal conductance were observed, the stomata-first path might, however, be more appropriate.

Recent research has indicated that patchy stomatal closure in response to stress may lead to errors in the calculation of C_i and thus to misleading conclusions regarding the magnitude of diffusional versus biochemical limitations to photosynthesis (9). If drought, but not UV-B radiation, resulted in uneven stomatal closure then this could lead to an underestimate of the photosynthetic limitation imposed by the stomata (7). However, we have no evidence for such patchiness in this study and observed apparent direct effects on photosynthetic capacity.

Previous studies have shown that drought and UV-B radiation may damage electron transport in PSII (6, 14), and this may be observed by changes in AQE. In this study, UV-B radiation decreased AQE (from 50–100 μmol incident PPFD) by 20% in well-watered and 30% in drought-stressed plants. These differences were magnified if AQE was calculated from 0 to 100 μmol incident PPFD because of an increase in dark respiration for the drought treatment. No significant reductions in AQE were detected in the drought treatment yet reductions in A at saturating C_i indicated that drought increased the substrate regeneration limitations on A (23). These limitations, which generally arise due to a lack of light reaction products and/or enzyme limitations (23), may be more sensitive to the mild drought conditions used in this study or may have been more readily detected than direct effects on AQE by the methods employed.

Both drought and UV-B radiation altered the fundamental biochemical and photochemical processes of photosynthesis, and they elicited similar reductions in growth independently. However, no additive effects were observed on photosynthetic capacity, growth, or yield. These results suggest that UV-B radiation may significantly affect soybean growth and photosynthesis primarily when water availability is high and that these effects may be obscured by drought, when growth and yield are already reduced. Field studies conducted over a 6-year period have also shown that the effectiveness of UV-B radiation on soybean is strongly influenced by the concurrent temperature, precipitation patterns and visible irradiance (28). Therefore, the magnitude of the effect of increased solar UV-B radiation on soybean productivity may be modified by concurrent changes in global temperature and precipitation patterns.

ACKNOWLEDGMENTS

The authors wish to thank Drs. I. N. Forseth, W. G. Gold and L. Ziska for their helpful suggestions and review of this manuscript.

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