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Ultraviolet-B Radiation and Ozone Effects on Growth, Yield, and Photosynthesis of Soybean

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ABSTRACT

The projected increase in solar ultraviolet-B (UV-B) radiation due to depletion of stratospheric ozone (O_3) has caused concern regarding possible UV-B damage to crops. At the same time, tropospheric O_3 is projected to remain at concentrations that are known to damage crops. Since these two stressors may co-occur, experiments were performed to determine their separate and joint effects on crop growth, yield, and photosynthesis. Open-top chambers, equipped with filtered UV-B lamp systems, were used in 3 yr of field studies to treat soybean [*Glycine max* (L.) Merr.; 'Coker 6955', 'Essex', and 'S 53-34'] with supplemental UV-B radiation and/or O_3 from emergence through physiological maturity. Treatment levels of biologically effective UV-B radiation (UV-B_{BE}) simulated the increase in ground level UV-B for stratospheric O_3 depletion up to 37% (approximately a doubling of ambient UV-B_{BE}). Ozone treatment concentrations ranged from 14 to 83 nL L^{-1} (seasonal mean 12 h d^{-1} concentrations). Ultraviolet-B radiation did not affect soybean seed yield in any of the 3 yr of the study. In 1 yr, UV-B affected pod and seed number and pod weight, but the treatment means were not consistently related to the UV-B dose. No O_3 × UV-B interactions were found for any yield component at final harvest. Biweekly harvests of Essex during the growing season did not reveal any persistent effects of increased UV-B radiation on growth. Net carbon exchange rate (NCER), stomatal conductance, and transpiration of Essex soybean leaves were not suppressed by supplemental UV-B radiation. On the other hand, O_3 treatment consistently induced visible injury, suppressed NCER and water use efficiency, accelerated reproductive development, and suppressed growth and yield. It is concluded that tropospheric O_3 poses a greater threat to soybean production than projected levels of UV-B radiation.

REDUCTIONS in the stratospheric O_3 layer due to emissions of chlorofluorocarbons and other trace gases and the resultant increase of solar UV-B radiation at the earth's surface has become a concern in recent years (Albritton, 1989; van der Leun et al., 1991; Stolarski et al., 1992). Studies have reported that UV-B radiation can affect plant growth and physiological function (Caldwell et al., 1989) and that effects are modified by other environmental factors (Tevini and Teramura, 1989). For example, UV-B effects on soybean have been reported to be reduced by water stress (Murali and Teramura, 1986), nutrient deficiency (Murali and Teramura, 1987), and visible light (Warner and Caldwell, 1983).

Although stratospheric O_3 is decreasing, concentrations of O_3 in the troposphere are stable or increasing (Fishman, 1991). Current levels of tropospheric O_3 are known to alter biochemical and physiological function of plants (Heath, 1988; Miller, 1988) and to suppress plant growth and yield (Heagle, 1989; Heck et al., 1991). For example, it has been estimated that soybean yields are suppressed ≈10% or more by 50 nL L^{-1} O_3 (seasonal mean 7 h d^{-1} concentration), an O_3 level that occurs frequently in areas where soybean is grown (Heagle, 1989). Also, because solar UV drives photolysis of NO_2 that leads to the production of O_3 in the troposphere, it is possible that elevated UV-B radiation will further increase ground-level O_3 in some areas (Thompson et al., 1991).

Since elevated levels of UV-B radiation and damaging concentrations of tropospheric O_3 may occur concurrently at ground level, their combined effects are of interest. In one published report, the combination of O_3 and UV-B radiation suppressed pollen tube growth approximately additively in tobacco (*Nicotiana tabacum* L.) and garden petunia (*Petunia hybrida* Vilm.) (Feder and Shrier, 1990). To conduct experiments on the effects of O_3 and UV-B radiation on the growth and yield of plants in the field, open-top chambers were equipped with filtered UV lamp banks (Booker et al., 1992a). Field studies were chosen so the plants would be exposed to near-normal visible light levels because plant response to UV-B radiation is dependent on visible light levels. The objectives of the work reported herein were to determine if soybean growth and yield are affected by enhanced UV-B radiation and to determine if interactive effects of O_3 and enhanced UV-B radiation might occur.

METHODS AND MATERIALS

Plant Culture

Three Group V soybean cultivars (Essex, Coker 6955, and S 53-34) were used in 1989 and 1990, and one cultivar (Essex) was used in 1991. Seeds were inoculated with *Bradyrhizobium* and sown in 15-L pots containing a 2:1:1 mixture of clayey-loam topsoil (Appling, clayey, kaolinitic, thermic Typic Kanhapludult)/sand/Metro Mix 220 (Grace Horticultural Products, W.R. Grace & Co., Cambridge, MA) on 30 June 1989, 31 May 1990, and 6 June 1991. Plants were thinned to a final density of two plants per pot in 1989 and to one plant per pot in 1990 and 1991. Each pot received 1 L of a nutrient solution containing 10–30–20 (N–P–K) soluble fertilizer (2.5 g L^{-1}; Peters Fertilizer Products, W.R. Grace & Co., Fogelsville, PA) at approximately 2-wk intervals; the initial application included S.T.E.M. micronutrient fertilizer (0.31 g L^{-1}; Peters Fertilizer Products). All plants in the experiments were irrigated on a regular basis to prevent water stress. Insects and mites were controlled with one application of Capture (bifenthrin; (2 methyl[1,1′-biphenyl]-3-yl) methyl 3-(2-chloro-3,3,3-trifluoro-1-propenyl)-2,2-dimethylcyclopropanecarboxylate) 3.2 EC (at a rate of 3.1 mL L^{-1}) and two applications of Talstar

Abbreviations: UV-B, ultraviolet-B; O_3, ozone; UV-B_{BE}, biologically effective UV-B radiation; NCER, net carbon exchange rate; UV, ultraviolet; CF, charcoal-filtered air; NF, nonfiltered air with no added O_3; OZ, O_3 added to NF air to achieve ≈1.5 times ambient O_3; RB, Robertson-Berger; PAR, photosynthetically active radiation; g_s, stomatal conductance; Trn, transpiration; ANOVA, analysis of variance; DAP, days after planting; WUE, water use efficiency.

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Table 1. Monthly mean temperatures, photosynthetically active radiation (PAR), ambient ozone (O_3) concentrations, biologically effective solar UV-B irradiance (UV-B_{BE}), rainfall, and irrigation during the studies in 1989, 1990, and 1991.

		Month					
Variable	Year	June†	July	Aug.	Sept.	Oct.	Total
	1989	—	30.7	29.2	27.1	22.9	
Mean max. temp., °C	1990	30.3	32.6	30.9	28.6	24.6	
	1991	31.8	33.9	31.5	29.1	24.0	
	1989	—	20.4	19.9	17.1	9.6	
Mean min. temp., °C	1990	17.7	20.7	20.2	16.1	11.0	
	1991	18.5	22.0	20.5	15.7	9.2	
	1989	—	21.3	20.3	17.6	10.3	
Mean dew point	1990	17.5	20.2	20.2	15.7	11.8	
temp., °C	1991	18.6	20.2	18.9	16.0	11.2	
	1989	—	33.2	27.0	22.9	27.3	
Mean PAR, mol	1990	40.0	38.6	30.1	27.1	24.0	
m^{-2} d^{-1}‡	1991	39.1	36.6	29.0	30.5	23.7	
	1989	—	53.2	43.2	37.8	34.7	
Mean O_3, nL L^{-1}§	1990	63.7	54.7	55.9	55.7	36.0	
	1991	54.7	52.1	44.3	43.0	34.1	
	1989	—	4.08	3.39	2.58	2.57	
Mean UV-B_{BE}, kJ	1990	4.72	4.73	3.58	3.14	2.28	
m^{-2} d^{-1}	1991	4.67	4.46	3.66	3.31	2.14	
	1989	—	13.1	16.9	12.0	10.0	52.0
Rainfall, cm	1990	3.2	9.4	11.9	0.5	13.2	38.2
	1991	14.4	11.3	13.1	5.2	2.4	46.4
	1989	—	15	50	61	23	149
Irrigation, L pot^{-1}	1990	21	54	96	88	31	290
	1991	9	26	44	58	10	147

† Environmental data for June 1989 is not included since soybeans were planted on 30 June 1989.
‡ PAR values are calculated from daily summations of the 24 hourly mean values.
§ Ambient ozone concentrations are 12 h d^{-1} means (0800–2000 EST).

(bifenthrin) 10 WP (1.57 g L^{-1}; Capture and Talstar, FMC Corporation, Philadelphia, PA) between 10 July and 7 Sept. 1989, four applications of Talstar between 12 June and 29 August 1990, and one application of Talstar and five of Orthene (acephate; *O,S*-dimethyl acetylphosphoramidothioate; Chevron Chemical Co., San Ramon, CA) 9.4 EC (11.7 mL L^{-1}) between 14 June and 16 Sept. 1991.

Pots were arranged symmetrically around the center of each open-top chamber. In 1989 four pots of each cultivar were randomly placed so that one pot of each cultivar was present in each of four quadrants. These 12 experimental pots were bordered with eight additional pots for shading and protection. In 1990 the north half of each chamber was used for yield determination with one pot of each cultivar randomly placed in each of three sectors. The south half of each chamber initially contained 10 pots of Essex, which were sequentially harvested throughout the season. Ten additional pots served as borders. In 1991 there were 22 pots of Essex arranged in four groups: a center section of seven pots for yield determination and three outer sectors of five pots each for sequential harvests. These in turn were ringed by eight border pots. During all 3 yr, wheat straw was placed around and between the pots to provide thermal insulation. Environmental conditions during the 3 yr of the study are shown in Table 1.

Ozone and Ultraviolet-B Treatments

Ozone was dispensed in 1989 and 1990 using open-top chambers covered with clear polyvinyl chloride film panels (Heagle et al., 1979a). Ozone treatments were CF, NF, and OZ as described by Heagle et al. (1986). Ozone was added for 12 h d^{-1} (0800 to 2000 EST) from 7 July to 15 Oct. 1989 and 4 June to 9 Oct. 1990. In 1991 the chamber frames were not covered with polyvinyl chloride panels, and the plants were exposed to ambient O_3.

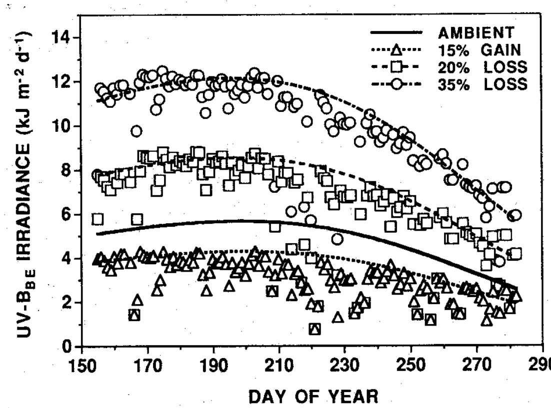

Fig. 1. Seasonal model calculations (lines) and daily UV-B_{BE} irradiances (symbols) for ambient and UV-B treatments in 1990. Daily ambient irradiance values not shown. Model projections were calculated with the Bjorn and Murphy (1985) radiative transfer model for ambient conditions on a clear day and for stratospheric O_3 losses of 20 and 35% in the UV-B supplements. The control treatment approximated a stratospheric O_3 addition of 15% (due to shading by the light bank assembly and chamber panels).

Supplemental UV-B radiation was supplied in the chambers by banks of commercially available UVB-313 fluorescent lamps (Q-Panel Co., Cleveland, OH) (Booker et al., 1992a). One lamp bank consisting of 14 lamps was suspended in each chamber. A pulley system was used to maintain the lamp bank at a prescribed height above the plant canopy (0.4 m). In the supplemental UV-B radiation treatments, a filter of 0.13 mm thick cellulose diacetate film (Cadillac Plastic & Chemical Co., Baltimore, MD), which absorbed emitted radiation below 292 nm, covered each lamp. In the control treatment, lamps were covered with filters of 0.13 mm thick polyester film, which absorbed emitted radiation below 315 nm. Because of photodegradation, resulting in decreased UV transmission, cellulose diacetate filters were replaced about three times each week in the high UV-B treatment and once a week in the medium UV-B treatment. Polyester filters were replaced monthly.

Lamp bank outputs were set by adjusting the input voltage to dimming ballasts based on measurements of lamp irradiance made with a portable erythemal meter (Model 2D, Solar Light Co., Philadelphia, PA). Outputs were adjusted each day in the supplemental UV-B treatments to maintain desired UV-B irradiances. The portable meter was calibrated against a spectroradiometer (Model 742, Optronic Laboratories, Orlando, FL). Biologically effective UV-B irradiance was calculated by applying the generalized plant action spectrum (Caldwell, 1971), normalized to 300 nm, to the spectroradiometer scans. Ambient solar UV radiation was monitored continuously in 1990 and 1991 with a Robertson-Berger (RB) meter (Solar Light Co., Philadelphia, PA). The RB meter output was calibrated against the spectroradiometer. On days for which RB counts were missing, ambient solar UV-B_{BE} was estimated from the observed relationship between RB counts and daily photosynthetically active radiation (PAR). Ambient solar UV-B_{BE} irradiance for 1989 was estimated from the RB count/PAR relationship observed for the 1990–1991 data. For those days with missing values for PAR, total solar radiation was estimated using a model described by Cengiz et al. (1981).

The total daily flux of supplemental UV-B radiation and exposure duration were adjusted biweekly to follow seasonal changes in photoperiod and predicted solar UV-B irradiance. The UV-B treatments were suspended on cloudy days to prevent abnormally high UV-B to PAR ratios when irradiance dropped below 50 mW m^{-2} for 30 min (suspended for 13, 15, and 13% of the planned treatment periods in 1989, 1990, and 1991, respectively). Supplemental UV-B radiation was administered as a constant addition at three levels in 1989 (6 July–15 Oct.) and at two levels in 1990 (4 June–9 Oct.) and 1991 (13 June–8 Oct.).

Supplemental UV-B radiation treatments and column O_3 loss simulations were computed with a radiative transfer model (Bjorn and Murphy, 1985) using values of 1002 mb for barometric pressure, 54% for relative humidity, and 1 for aerosol level (Booker et al., 1992b). The additions simulated the daily solar UV-B_{BE} irradiances corresponding to stratospheric O_3 depletions of ≈4, 20, and 32% in 1989; ≈20 and 35% in 1990; and ≈23 and 37% in 1991. The control treatment corresponded to an increase of column O_3 thickness of 15% (24% decrease in UV-B irradiance) in 1989 and 1990 due to shading of ambient UV-B radiation by light bank assemblies and chamber panels, and ≈9% (16% decrease in UV-B irradiance) in 1991 when chamber panels were not present.

The experimental design in 1989 was a completely randomized factorial split-plot (cultivar was the subplot) with three O_3 treatments and four UV-B treatments replicated twice. The NF treatment was unreplicated, so there were a total of 20 open-top chambers used. The 1990 design was similar, but with three UV-B treatments and four replicates except for the NF treatment, which was replicated twice (total of 30 chambers). In 1991 the experiment was performed under ambient O_3. There were three replicates of three UV-B treatments in a completely random design.

Plant Sampling and Measurements

Visible foliar injury was evaluated on at least three dates in each of the 3 yr. Injury estimates were the combined percentages of leaf area affected by chlorosis and necrosis (0–100% in 5% increments) on the eight youngest fully-expanded mainstem trifoliolates on two plants of each cultivar per plot in 1989 and 1990. In 1991 injury estimates were made at 3-wk intervals from 29 July to 1 October on three plants per plot. Growth stage was estimated according to Fehr and Caviness (1977).

Plants were harvested at physiological maturity for yield measurements (13 Nov. 1989, 6 Nov. 1990, and 24 Oct. 1991). In 1989 and 1990 plants were air dried and the pods were mechanically threshed. Seed yield and number per plant and weight per 100 seeds were obtained. Yield measurements in 1991 were obtained at the final harvest of the growth study. Processing of pods and seeds was similar to that of 1989–1990 except plants were separated into their component tissues immediately after removal from the field, and tissues were oven dried to constant weight at 80 °C prior to weighing.

In addition to yield measurements, growth data were collected for Essex in 1990 and 1991. There were 10 sequential harvests in 1990 (12 and 19 June; 3, 17, and 31 July; 14 and 29 Aug.; 12 and 26 Sept.; and 10 Oct.) and seven in 1991 (21 June, 9 and 29 July, 20 Aug., 11 Sept., and 2 and 24 Oct.). One plant was randomly sampled from the south half of each plot on each harvest date in 1990. In 1991, three plants from each plot, one randomly selected from each of the three outer sectors, were sampled on each harvest date. Plants were separated into mainstem and branch leaves, branches (including petioles), mainstem (including petioles), roots, and pods. Tissues were oven dried to constant weight and weighed. Leaf areas were measured with a LI-3100 area meter (LI-COR, Lincoln, NE). Data for mainstem height and numbers of mainstem nodes, branches, mainstem leaves, and branch leaves were also collected.

Measurements of NCER, g_s, and Trn were made with a LI-6000 portable photosynthesis system, software version 2.00 (LI-COR). In 1990 the uppermost fully-expanded mainstem trifoliolate of Essex was sampled. Measurements were made on three plants in each of two plots for all UV-B combinations with the CF and OZ treatments. In 1991 trifoliolates at the second mainstem node (down from the apex) were sampled on four Essex plants in each of the nine plots.

Statistical Analyses

Analysis of variance was performed on all yield parameters for individual years. In 1989 and 1990, ANOVAs were used to test the effects of O_3, UV-B radiation, cultivar and their interactions, with cultivar treated as the subunit of a split-plot design. In 1991 UV-B was the only independent variable. Data from all parameters were analyzed for nonnormality and heterogeneous error variances prior to running the ANOVAs (Rawlings, 1988). Similar ANOVAs were performed on NCER, g_s, Trn, and visible injury data for each of the sampling dates. Analyses of variance also were done on all growth parameters for each sequential harvest date in 1990 and 1991. Statistical significance was defined at $\alpha = 0.05$.

RESULTS

UV-B Doses

Seasonal model projections for UV-B_{BE} and daily UV-B_{BE} irradiances for the 1990 experiment are shown in Fig. 1. The results were similar in 1989 and 1991. Mean daily UV-B_{BE} irradiances for the experimental periods in the UV-B treated plots were 2.47 (control), 3.88, 5.63, and 7.32 kJ m^{-2} in 1989; 3.02 (control), 6.24, and 8.98 kJ m^{-2} in 1990; and 3.27 (control), 6.41, and 9.27 kJ m^{-2} in 1991. Mean daily ambient UV-B_{BE} irradiances for the experimental periods were 3.25, 3.98, and 3.90 kJ m^{-2} for 1989, 1990, and 1991, respectively.

Visible Injury

There were some indications that elevated UV-B radiation slowed the development of symptoms of visible injury associated with O_3 exposure. In 1990 the O_3 × UV-B radiation interaction was significant on 75 DAP (Table 2). In this case visible injury values in the OZ treatment were the greatest in the low UV-B treatments. The O_3 × UV-B × cultivar effect was significant on the third sample date with injury usually the greatest in the low UV-B treatments in the NF and OZ plots. Ozone effects and O_3 × cultivar interactions were significant on all three dates. In 1989 UV-B radiation occasionally suppressed visible injury in the OZ plants (data not shown), as in 1990. In 1991, no significant UV-B effects on visible injury were detected at ambient O_3 concentrations (data not shown).

Yield/Biomass at Harvest

No O_3 × UV-B interactions nor O_3 × UV-B × cultivar interactions were found for any yield component at final harvest in 1989 or 1990 (Table 3). Ultraviolet-B effects were detected for pod number, seed number, and pod weight in 1989. There was no consistent UV-B treatment-related pattern to these effects, although pod weights were usually the greatest in plants in the three highest UV-B treatments in 1989 (Table 4). This pattern did not occur in 1990 (Table 5). In the 1991 study with Essex, no significant UV-B effects were found at ambient O_3 levels in the absence of open-top chamber panels (Tables 3 and 6).

Ozone consistently suppressed yield components of all three cultivars in 1989 and 1990 (Tables 3, 4, and 5).

Table 2. Visible injury to leaves of Coker 6955 (C), Essex (E), and S 53-34 (S) soybean treated with chronic doses of O_3 and UV-B radiation in 1990, and mean squares and probability levels from the analyses of variance for each evaluation date.†

O_3	UV-B	61 DAP‡ (31 July) C	E	S	75 DAP (14 August) C	E	S	89 DAP (28 August) C	E	S
nL L^{-1}§	kJ m^{-2}¶	% visible injury								
24 (CF)	3.02	0.0	0.0	0.0	0.0	0.0	0.0	0.1	2.8	2.0
	6.24	0.0	0.0	0.0	0.0	0.0	0.0	0.4	2.0	3.8
	8.98	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.9	1.2
49 (NF)	3.02	0.0	0.0	0.3	1.3	1.7	3.4	10.5	10.3	15.0
	6.24	0.0	0.0	0.0	1.3	1.6	3.1	8.0	9.7	9.5
	8.98	0.0	0.0	0.0	1.4	2.2	2.2	7.3	8.3	12.5
83 (OZ)	3.02	4.9	12.1	15.5	40.3	41.7	43.0	62.6	63.0	63.4
	6.24	7.7	8.6	11.7	35.7	30.9	40.0	59.8	50.0	62.3
	8.98	3.8	7.0	12.0	35.5	33.2	40.2	59.9	56.9	63.2

Source	df	61 DAP Mean square	$P > F$	75 DAP Mean square	$P > F$	89 DAP Mean square	$P > F$
O_3	2	4128	0.0001	14944	0.0001	34014	0.0001
UV-B	2	44	0.0634	41	0.0374	57	0.0247
O_3 × UV-B	4	35	0.0719	40	0.0184	29	0.0981
Error *a*#	21	14		11		13	
cv	2	120	0.0083	40	0.0015	80	0.0001
O_3 × cv	4	306	0.0001	28	0.0013	37	0.0013
UV-B × cv	4	5	0.9257	4	0.5363	8	0.3431
O_3 × UV-B × cv	8	16	0.6853	6	0.3777	16	0.0363
Error *b*††	42	22		5		7	

† Each value is the mean of the combined percentages of chlorosis and necrosis (0–100%, in 5% increments) on the eight youngest fully-expanded mainstem trifoliolates on two plants of each cultivar per plot. Each value for 24 and 83 nL L^{-1} O_3 treatments is the mean of eight plants (two from each of four plots); each 49 nL L^{-1} O_3 treatment value is the mean of four plants (two from each of two plots). Analyses of variance were run on plot values for each evaluation date.
‡ DAP = days after planting.
§ Ozone concentrations are seasonal 12 h d^{-1} means (0800–2000 EST, 4 June to 9 October) for the charcoal-filtered air (CF), nonfiltered air (NF), and 1.5 × ambient O_3 (OZ) treatments, respectively. Mean daily ambient O_3 for the same period was 56 nL L^{-1}.
¶ These values represent seasonal mean daily $UV\text{-}B_{BE}$ irradiance in the three treatments from 4 June to 9 October. Mean daily ambient $UV\text{-}B_{BE}$ irradiance for the same period was 3.98 kJ m^{-2}. The total daily flux of supplemental UV-B radiation and exposure duration were adjusted biweekly to follow seasonal changes in photoperiod and solar UV-B irradiance.
\# Error *a* is the Rep(O_3 × UV-B) mean square and tests significance levels of O_3, UV-B and their interaction.
†† Error *b* is the Rep(O_3 × UV-B × CV) mean square and tests significance levels of cv and cv interactions with O_3 and UV-B.

Table 3. Mean squares and probability levels from analyses of variance for yield components of Coker 6955 (1989–1990), Essex (1989–1991), and S 53-34 (1989–1990) soybean for 3 yr.†

Source	df	Pod number Mean square	$P > F$	Pod weight Mean square	$P > F$	Seed number Mean square	$P > F$	Seed yield Mean square	$P > F$	100 Seed weight Mean square	$P > F$
					1989						
O_3	2	28140	0.0001	25107	0.0001	180098	0.0001	15712	0.0001	81.43	0.0001
UV-B	3	3027	0.0451	485	0.0445	15678	0.0479	223	0.1335	0.20	0.7376
O_3 × UV-B	6	631	0.5458	76	0.6789	5360	0.3160	61	0.6714	0.44	0.5029
Error *a*‡	8	712		114		3785		89		0.46	
cv	2	17280	0.0001	424	0.0648	11819	0.2136	353	0.0311	0.88	0.1369
O_3 × cv	4	5084	0.0001	842	0.0027	17113	0.0870	501	0.0034	3.18	0.0009
UV-B × cv	6	162	0.7843	41	0.9188	3407	0.8058	25	0.9214	0.38	0.4802
O_3 × UV-B × cv	12	237	0.6800	87	0.7567	3787	0.8538	47	0.8267	0.44	0.4044
Error *b*§	16	312		130		6942		81		0.39	
					1990						
O_3	2	64957	0.0001	83272	0.0001	332157	0.0001	43535	0.0001	266.51	0.0001
UV-B	2	2069	0.3125	114	0.7728	2558	0.7085	67	0.7803	0.27	0.6622
O_3 × UV-B	4	345	0.9329	224	0.7262	3086	0.7905	150	0.6909	0.32	0.7361
Error *a*	21	1681		435		7299		266		0.63	
cv	2	95217	0.0001	13548	0.0001	171629	0.0001	6696	0.0001	7.12	0.0001
O_3 × cv	4	3020	0.0912	244	0.5438	18279	0.0358	124	0.5772	2.21	0.0028
UV-B × cv	4	721	0.7259	304	0.4327	3839	0.6668	169	0.4218	0.25	0.7081
O_3 × UV-B × cv	8	1398	0.4532	275	0.5427	5781	0.5262	176	0.4263	0.74	0.1539
Error *b*	42	1403		313		6431		170		0.46	
					1991						
UV-B	2	52	0.6688	3.26	0.8438	208	0.7405	1.06	0.9190	0.52	0.2151
Error	6	121		18.63		657		12.37		0.26	

† Analyses run on plot values, which are means of four plants per cv per plot in 1989, three plants per cv per plot in 1990, and seven plants per plot in 1991.
‡ Error *a* is the Rep(O_3 × UV-B) mean square and tests significance levels of O_3, UV-B and their interaction.
§ Error *b* is the Rep(O_3 × UV-B × cv) mean square and tests significance levels of cv and cv interactions with O_3 and UV-B.

Table 4. Effects of chronic doses of O_3 and UV-B radiation on yield components of three soybean cultivars in 1989.†

		Coker 6955					Essex					S 53-34				
O_3	UV-B	Pod no.	Seed no.	Pod wt.	Seed yield	100 Seed wt.	Pod no.	Seed no.	Pod wt.	Seed yield	100 Seed wt.	Pod no.	Seed no.	Pod wt.	Seed yield	100 Seed wt.
nL L^{-1}‡	kJ m^{-2}§			g					g					g		
14 (CF)	2.47	363	760	160.6	122.7	15.87	370	844	166.8	125.5	16.02	328	684	166.3	125.8	16.87
	4.24	402	762	187.4	141.8	17.98	352	717	158.1	117.2	15.88	327	810	166.3	123.6	16.81
	6.36	369	652	163.1	123.4	16.13	364	716	166.2	123.4	16.50	334	760	162.5	120.7	16.07
	8.29	405	807	180.6	137.6	17.12	390	882	180.4	136.5	16.82	368	806	178.5	134.8	15.97
36 (NF)	2.47	411	871	182.7	140.4	16.13	335	650	146.2	111.7	16.17	299	751	140.4	105.6	15.60
	4.24	433	919	185.0	139.1	15.98	398	761	176.7	129.5	15.43	345	812	158.6	115.3	15.63
	6.36	385	728	166.3	124.9	16.54	346	684	160.2	116.6	16.54	281	671	151.3	108.3	15.37
	8.29	431	821	181.8	136.5	15.35	372	796	172.8	128.2	16.29	324	726	153.3	111.3	15.35
64 (OZ)	2.47	303	587	94.8	69.5	11.62	268	565	96.7	70.9	13.07	292	634	117.8	85.7	13.25
	4.24	353	666	110.3	80.6	11.52	262	544	98.7	73.0	13.77	303	626	119.9	86.3	13.32
	6.36	333	638	108.3	78.7	12.27	252	514	96.8	71.8	13.91	311	660	125.6	91.1	13.44
	8.29	350	630	113.8	82.2	12.20	267	557	98.9	71.7	13.60	323	677	127.7	90.9	13.54

† Each value for 14 and 64 nL L^{-1} O_3 treatments is the mean of eight 15-L pots (four from each of two plots) with two plants per pot; each 36 nL L^{-1} O_3 treatment value is the mean of four pots from a single plot.
‡ Ozone concentrations are seasonal 12 h d^{-1} means (0800–2000 EST, 7 July to 15 October) for the charcoal-filtered air (CF), nonfiltered air (NF), and 1.5 × ambient O_3 (OZ) treatments, respectively. Mean daily ambient O_3 concentration for the same period was 43 nL L^{-1}.
§ These values represent seasonal mean daily UV-B$_{BE}$ irradiance in the four treatments from 6 July to 15 October. Mean daily ambient UV-B$_{BE}$ irradiance for the same period was 3.25 kJ m^{-2}. The total daily flux of supplemental UV-B radiation and exposure duration were adjusted biweekly to follow seasonal changes in photoperiod and solar UV-B irradiance.

Significant O_3 × cultivar interactions indicated the effects sometimes differed across cultivars.

Growth Analysis

In the 1990 and 1991 studies, Essex soybean were harvested at intervals to determine treatment effects on growth and biomass throughout the season. In 1990, three O_3 × UV-B interactions were detected (mainstem and total plant dry weight at 19 DAP and branch dry weight at 61 DAP). None of these showed any treatment related pattern and were considered to be the result of random variability (data not shown). Effects of UV-B were indicated at 47 DAP for root dry weight (decrease in higher UV-B treatments) and branch number (no pattern). Since these effects were not observed at subsequent harvests, they were either fortuitous or transient occurrences. In all, only five significant tests (ANOVA, $\alpha = 0.05$) for UV-B or O_3 × UV-B were found out of a total of 244 tests, which is within the range of chance alone. In 1991, no UV-B effects were found on any measured plant growth variable at ambient O_3 (data not shown).

Ozone treatments, on the other hand, caused substantial and consistent suppression of plant growth. Since UV-B effects and interaction with O_3 were almost always nonsignificant, the data for plants in the UV-B treatments were combined within O_3 treatments. Growth curves for total plant, leaf, and pod dry weights illustrate the effects of O_3 (Fig. 2). Pod dry weight was initially stimulated by O_3 due to earlier initiation of reproductive growth

Table 5. Effects of chronic doses of O_3 and UV-B radiation on yield components of three soybean cultivars in 1990.†

		Coker 6955					Essex					S 53-34				
O_3	UV-B	Pod no.	Seed no.	Pod wt.	Seed yield	100 Seed wt.	Pod no.	Seed no.	Pod wt.	Seed yield	100 Seed wt.	Pod no.	Seed no.	Pod wt.	Seed yield	100 Seed wt.
nL L^{-1}‡	kJ m^{-2}§			g					g					g		
24 (CF)	3.02	455	884	238.6	171.7	19.41	385	818	201.2	146.0	17.74	373	816	203.4	145.6	17.94
	6.24	489	962	248.7	181.0	19.56	377	783	190.5	139.1	17.72	348	704	188.1	136.3	17.99
	8.98	467	880	230.0	160.2	18.23	384	789	194.5	141.5	17.76	376	814	204.8	146.4	18.03
49 (NF)	3.02	449	854	198.8	141.9	16.70	380	786	175.9	126.3	16.05	338	736	166.6	119.8	16.24
	6.24	472	925	223.6	160.5	17.64	370	790	179.4	131.2	16.65	376	809	177.0	125.6	15.52
	8.98	469	883	216.9	157.5	18.07	368	750	168.3	123.0	16.38	412	883	191.6	137.0	15.43
83 (OZ)	3.02	394	784	140.7	101.6	12.92	251	504	89.6	64.4	12.67	310	647	115.0	81.5	12.58
	6.24	394	747	134.1	96.6	12.92	285	572	105.5	76.3	13.26	301	614	110.1	78.5	12.79
	8.98	436	828	147.7	106.3	12.87	273	545	96.4	69.2	12.63	310	639	118.3	84.6	13.25

† Each value for 24 and 83 nL L^{-1} O_3 treatments is the mean of 12 plants (three from each of four plots) grown individually in 15-L pots; each 49 nL L^{-1} O_3 treatment value is the mean of six plants (three from each of two plots).
‡ Ozone concentrations are seasonal 12 h d^{-1} means (0800–2000 EST, 4 June to 9 October) for the charcoal-filtered air (CF), nonfiltered air (NF), and 1.5 × ambient O_3 (OZ) treatments, respectively. Mean daily ambient O_3 concentrations for the same period was 56 nL L^{-1}.
§ These values represent seasonal mean daily UV-B$_{BE}$ irradiance in the three treatments from 4 June to 9 October. Mean daily ambient UV-B$_{BE}$ irradiance for the same period was 3.98 kJ m^{-2}. The total daily flux of supplemental UV-B radiation and exposure duration were adjusted biweekly to follow seasonal changes in photoperiod and solar UV-B irradiance.

Table 6. Effects of chronic doses of UV-B radiation on yield components of Essex soybean in 1991.†

O_3	UV-B	Pod no.	Seed no.	Pod wt.	Seed yield	100 Seed wt.
nL L^{-1}‡	kJ m^{-2}§			g		
43	3.27	286	537	121.51	91.71	16.95
	6.41	278	534	119.63	90.57	17.07
	9.27	280	522	121.35	91.44	17.72

† Each value is the mean of 21 plants (seven from each of three plots) grown individually in 15-L pots.
‡ Ozone concentration is seasonal 12 h d^{-1} mean (0800–2000 EST) for ambient air in the plots.
§ These values represent seasonal mean daily UV-B_{BE} irradiance in the three treatments from 13 June to 8 October. Mean daily ambient UV-B_{BE} irradiance for the same period was 3.90 kJ m^{-2}. The total daily flux of supplemental UV-B radiation and exposure duration were adjusted biweekly to follow seasonal changes in photoperiod and solar UV-B irradiance.

(Fig. 2d), while it was suppressed later in the growing season (Fig. 2c). Partitioning of biomass was altered by O_3 to favor shoot development as illustrated by root weight ratios (root dry weight/total dry weight) (Fig. 3).

Development

The effects of UV-B on the rate of reproductive development were negligible in all three years of the study (data not shown). Ozone, on the other hand, accelerated reproductive development as indicated by R stages in 1990 (Table 7). The main effects of O_3 were significant on all dates. The effects of cultivar and the O_3 × cultivar interaction were significant except for 117 and 130 DAP.

Gas Exchange

Leaf gas exchange characteristics (NCER, g_s, and Trn) of Essex soybean were measured on 8 and 5 d during reproductive development in 1990 and 1991, respectively. The UV-B treatments (main effects) did not suppress measures of gas exchange in either year. In 1991 on 71 DAP, NCER values were 8 to 10% greater in leaves from the two higher UV-B treatments compared with the low UV-B treatment. In 1990 at 97 DAP, an O_3 × UV-B interaction was found for NCER. In the OZ treatment, NCER values were 13 to 25% less for leaves in the two higher UV-B treatments than for leaves in the low UV-B treatment. Transpiration was not affected by UV-B on either year. In 1990 on 88 and 102 DAP, g_s values were 5 to 36% greater in the enhanced UV-B treatments compared to the low UV-B treatment.

Since UV-B effects on gas exchange were uncommon, data from the UV-B treatments in 1990 were combined within the two O_3 treatments (Fig. 4). In contrast to the infrequent effects of UV-B, O_3 suppressed leaf NCER on all but the first measurement date. Transpiration and g_s were suppressed on the last six dates.

The NCER/transpiration ratio [leaf water use efficiency (WUE)] was calculated from the 1990 data to determine if effects were primarily on stomates or on

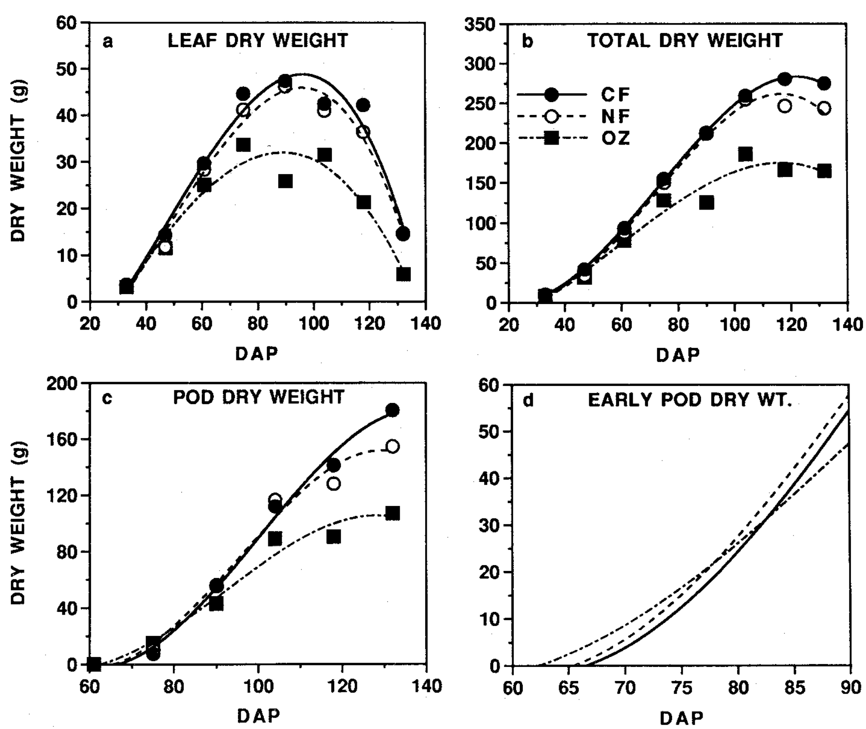

Fig. 2. Growth data (g plant^{-1}) and growth curves for 'Essex' soybean grown in charcoal-filtered air (CF), nonfiltered air (NF), or 1.5 times ambient O_3 (OZ) in 1990. Data were combined across UV-B treatments. DAP = days after planting. Growth curves are third-order polynomial equations fit to data from 12 plants in the CF and OZ treatments and six plants in the NF treatment at each sampling date. Ozone treatment differences are statistically significant (α = 0.05) for each harvest date beginning at 33 DAP for total dry weight, 47 DAP for leaf dry weight, and 75 DAP for pod dry weight. Growth curve coefficients of determination (R^2) are CF = 0.93, NF = 0.95, OZ = 0.81 for leaf dry weight; CF = 0.96, NF = 0.96, OZ = 0.91 for total dry weight; and CF = 0.95, NF = 0.92, OZ = 0.90 for pod dry weight.

Table 7. Effects of chronic doses of O_3 on reproductive stages of three soybean cultivars in 1990.†

Cultivar	O_3	Days after planting								
		53	67	74	81	89	117	123	130	138
	nL L^{-1}‡	R stage§								
Coker 6955	24 (CF)	0.6	3.0	3.6	5.0	5.0	6.0	6.3	7.0	7.5
	49 (NF)	0.7	3.0	3.3	5.0	5.0	6.0	6.0	7.0	8.0
	83 (OZ)	1.7	3.0	4.1	5.0	5.6	6.1	7.3	7.9	8.0
Essex	24	1.6	3.0	4.9	5.0	6.0	6.0	6.4	7.0	8.0
	49	1.9	3.0	5.0	5.0	6.0	6.0	6.9	7.0	8.0
	83	2.0	3.6	5.0	5.5	6.0	6.5	7.3	7.9	8.0
S 53-34	24	0.0	2.2	3.1	5.0	5.0	6.0	6.0	7.0	7.2
	49	0.2	2.3	3.3	5.0	5.0	6.0	6.0	7.0	7.8
	83	1.0	3.0	4.2	5.0	5.8	6.1	7.1	7.8	8.0

† Each value for 24 and 83 nL L^{-1} O_3 treatments is the mean of 24 plants (two from each of 12 plots); each 49 nL L^{-1} O_3 treatment value is the mean of 12 plants (two from each of six plots). UV-B effects on reproductive development were negligible, so data were combined across UV-B treatments.

‡ Ozone concentrations are seasonal 12 h d^{-1} means (0800–2000 EST, 4 June to 9 October) for the charcoal-filtered air (CF), nonfiltered air (NF), and 1.5 × ambient O_3 (OZ) treatments, respectively. Mean daily ambient O_3 concentration for the same period was 56 nL L^{-1}.

§ Reproductive stages were evaluated on two plants of each cultivar per plot using the method of Fehr and Caviness (1977).

photosynthetic mechanisms (data not shown). Ozone treatment suppressed WUE (27–53%) on the last six measurement dates (88 through 116 DAP), whereas there were no effects of UV-B. On 97 DAP an O_3 × UV-B interaction resulted from the suppression of WUE by UV-B in the OZ treatments but not in the CF treatments.

DISCUSSION

In our studies we used the Bjorn and Murphy (1985) radiative transfer model to compute column O_3 loss and UV-B radiation treatments. The use of this model is preferable since it provides estimates of UV-B radiation that more closely match measured ambient UV-B radiation than the predictions computed with the model of Green et al. (1980) (E.L. Fiscus and F.L. Booker, 1993, personal communication). The consequences of using the Bjorn and Murphy (1985) model are that estimated column O_3 losses for given supplemental UV-B treatments will be higher than those in previous studies that used the Green et al. (1980) model. For example, a treatment of 5.1 kJ m^{-2} d^{-1} above ambient was reported as a 25% depletion of stratospheric O_3 on 21 June (Teramura et al., 1990), whereas the Bjorn and Murphy (1985) calculation indicates this is closer to a 35% depletion of stratospheric O_3. This difference must be kept in mind when comparing the present study to others. For this reason, it is preferable to compare treatments among studies using actual radiation exposures or enhancements.

Previous field research on the effects of supplemental UV-B radiation on soybean growth and yield has produced variable results. Teramura et al. (1990) reported the results of 6 yr of field studies with Essex and 'Williams'. They reported yield losses for Essex on 4 of 6 yr at a $UV\text{-}B_{BE}$ enhancement level of 5.1 kJ m^{-2} d^{-1} above ambient [simulating a 25% depletion of stratospheric O_3 at Beltsville, MD according to the Green et al. (1980) model]. The yield suppression averaged ≈20% during the 4 yr. At a $UV\text{-}B_{BE}$ enhancement level of 3.0 kJ m^{-2} d^{-1} above ambient (simulating a 16% depletion of stratospheric O_3), seed yield was suppressed once and stimulated twice in 6 yr of study. With Williams soybean, the higher UV-B level stimulated or suppressed yield in 1 yr each, whereas the lower UV-B level caused yield increases in 3 yr and a suppression in 1 yr. Yield of Essex was suppressed most during years when water was readily available, whereas the opposite seemed the

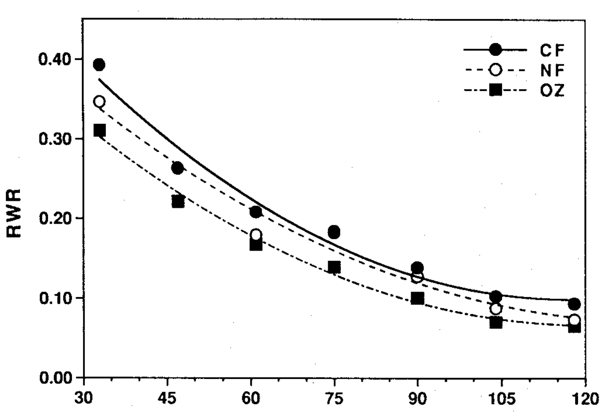

Fig. 3. Root weight ratio (RWR; root dry weight/total plant dry weight) for 'Essex' soybean grown in charcoal-filtered air (CF), nonfiltered air (NF), or 1.5 times ambient O_3 (OZ) in 1990. Data were combined across UV-B treatments. DAP = days after planting. Growth curves are second-order polynomial equations fit to data (33 through 118 DAP) from 12 plants in the CF and OZ treatments and six plants in the NF treatment at each sampling date. Ozone treatment differences are statistically significant (α = 0.05) at all sampling dates. Growth curve coefficients of determination (R^2) are CF = 0.96, NF = 0.94, OZ = 0.98.

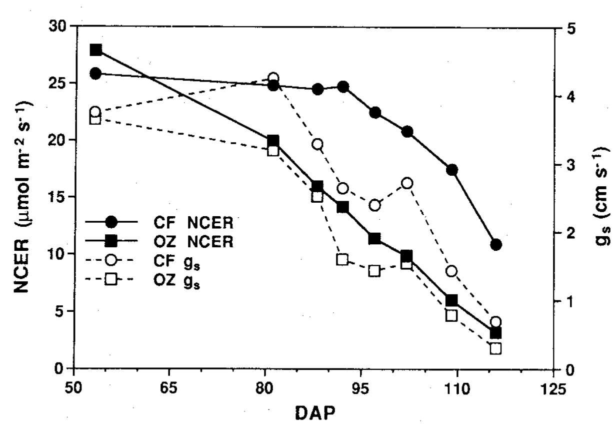

Fig. 4. Net carbon exchange rate (NCER) and stomatal conductance (g_s) for 'Essex' soybean leaves grown in charcoal-filtered air (CF) or 1.5 times ambient O_3 (OZ) in 1990. DAP = days after planting. Measurements were taken from the uppermost fully-expanded mainstem trifoliolate on three plants in each of two plots for all combinations of the three UV-B treatments with CF and OZ. Data were combined across UV-B treatments. Each data point is the mean of 13 to 18 measurements except on 23 July (53 DAP), when only nine were made in the CF treatment. Ozone treatment differences are statistically significant (α = 0.05) beginning at 81 DAP.

case with Williams. In another study with Essex, the greater sensitivity of seed yield to UV-B under well-watered as compared with water-stressed conditions was confirmed (Murali and Teramura, 1986), whereas in a later study it was not (Sullivan and Teramura, 1990). In a previous field study with six soybean cultivars, Teramura and Murali (1986) reported a 25% suppression of seed yield in 'York' due to UV-B_{BE} enhancement simulating a 16% depletion of stratospheric O_3 (Green et al., 1980), but no effects occurred in the other five cultivars, including Essex.

In another field study with six soybean cultivars, Sinclair et al. (1990) found no effects on final seed yield with UV-B_{BE} enhancement levels of 32% above ambient [simulating a 16% depletion of stratospheric O_3 at Gainesville, FL (Green et al., 1980)]. Furthermore, no effects on leaf area development, internode length, phyllochron index, flowering date, podding date, or crop growth rate were found.

In the present studies, suppression of yield by UV-B radiation was not found for any of three soybean cultivars (Essex, Coker 6955, and S 53-34) at seasonal mean UV-B_{BE} enhancements up to 5.37 kJ m^{-2} d^{-1} [simulating a 37% depletion of stratospheric O_3 according to the Bjorn and Murphy model (1985)]. More detailed analysis of vegetative and reproductive growth also failed to reveal any consistent or substantial suppression of growth by UV-B radiation.

The mean UV-B_{BE} irradiance enhancements for some of the treatments in our studies were fairly similar to those reported by Teramura et al. (1990). They reported UV-B_{BE} irradiation enhancements of 3.0 and 5.1 kJ m^{-2} d^{-1}. In our studies in 1989, the mean seasonal enhancements (with respect to measured mean seasonal ambient UV-B_{BE} levels) in the four UV-B treatments were −0.78 (less than ambient due to shading of chamber panels and light banks), 0.63, 2.38, and 4.07 kJ m^{-2} d^{-1}, respectively. Average values in 1990 were −0.96, 2.26, and 5.00 kJ m^{-2} d^{-1}. In 1991, the values were −0.63, 2.41, and 5.37 kJ m^{-2} d^{-1}. Our UV-B treatments were adjusted biweekly to simulate the seasonal ambient UV-B irradiance at projected decreases in the O_3 column. As seen in Fig. 1, enhancements were much lower in the late summer to simulate the normal decline in solar irradiance. If the same UV-B enhancement levels are given throughout the season, there is a disproportionately large ratio of UV-B compared with visible light in late summer or early fall months. Because soybean (Mirecki and Teramura, 1984) and other plants (Tevini and Teramura, 1989) are generally more sensitive to UV-B radiation when visible radiation is lower, it is important that UV-B doses be tailored to account for the seasonal changes in solar UV-B.

We and others have previously reported increased absorption in the UV wavelengths in leaf extracts from UV-B-treated plants, suggesting that flavonoids and other phenolics were increased by UV-B radiation treatment (Tevini and Teramura, 1989; Miller et al., 1991; Booker et al., 1992b). Other measured physiological responses, however, typically were not affected by enhanced UV-B radiation. For example, UV-B did not affect peroxidase activity or chlorophyll levels in the same plants used in the present studies or in a related study (Booker et al., 1992b).

Net carbon exchange rate and g_s were not suppressed by UV-B in the present study. Our measurements of gas exchange encompassed growth stages R2 through R7 and R4 through R6 in the 2 yr. The leaves had been exposed to enhanced UV-B from initial unfolding and up to 60 to 66 d. In contrast, Sullivan and Teramura (1990) previously reported a 16% suppression of NCER in field-grown Essex soybean at the R1 to R2 growth stage by UV-B_{BE} enhancement of 5.1 kJ m^{-2} d^{-1}. Seed yields were not affected by UV-B in that study although total plant dry weight was suppressed by 34%. The UV-B_{BE} enhancement levels were not greatly different between that study and ours, as previously discussed. In our studies, gas exchange measurements were made on the uppermost fully-expanded leaf (1990) or second leaf down from the apex (1991) on the mainstem to assure full exposure to the UV-B radiation treatments and sunlight. Sullivan and Teramura (1990) measured leaves at the seventh node position, which might be shaded much of the day from both sunlight and UV-B treatments. It is possible that there were differences in photorepair between the leaves measured in the two studies.

In contrast to UV-B, O_3 treatment consistently induced visible injury, suppressed NCER and WUE, accelerated reproductive development, and suppressed growth and yield. The effects of O_3 on seed yield of the three cultivars of soybean were within the range of effects previously reported. For example, at a concentration of 50 nL L^{-1} O_3 (seasonal 12 h d^{-1} mean), the relative suppression of yield was estimated to be 15 to 17% for all three cultivars based on a quadratic dose-response function. This compares with estimates of 15 to 21% suppression of soybean yield at the same O_3 level reported by Heck et al. (1991). In the latter case the soybean were grown in the ground, whereas in the current study the plants were grown in pots. Heagle et al. (1983) previously reported very similar relative yield suppression by O_3 when soybean were grown in pots or in the ground.

The reasons for the differences in response of soybean to UV-B radiation obtained in field studies at different locations is not clear. Differences in cultivar sensitivity (Teramura and Murali, 1986) might account for some of the differences in results. In the present study, Essex was one of the cultivars selected since it has been identified as fairly UV-B sensitive (Teramura et al., 1990). In our 3 yr of field studies, however, no effects of UV-B on seed yield of Essex were found at UV-B_{BE} levels of ≈5.1 kJ m^{-2} d^{-1} above ambient, which is very similar to the UV-B enhancements used by Teramura.

Differences in environmental conditions may also be a reason for the different responses of soybean to UV-B radiation that have been observed. As previously mentioned, Teramura et al. (1990) found that response of soybean to UV-B radiation correlated with water availability (i.e., suppression of yield of Essex occurred when water availability was greater). In our studies, the plants were well-watered throughout the entire season, so water availability probably did not limit response to UV-B. Some evidence suggests, however, that variations in environmental conditions do not always substantially influence response to aboveground stress. For example, even different environmental conditions that modified plant growth rates did not alter the percentage yield loss in soybean due to O_3 unless the plants were severely stunted (Heagle et al., 1983). Also, several studies have shown very similar relative yield responses to aboveground stress (O_3) whether plants were grown in the ground or in pots (Heagle et al., 1979b, 1983).

Open-top chambers, which were used in the first 2 yr of our studies, cause some alteration of the plant environment. Because of this, we performed a third experiment in 1991 in which open-top chamber panels were not placed on the chambers. Still, no effects of UV-B on growth and yield of Essex soybean were found. It seems that UV-B effects on soybean are subtle and perhaps variable results should be expected. Future work should concentrate on defining the conditions under which UV-B radiation may affect crop productivity.

SUMMARY

In 3 yr of field studies, enhanced UV-B radiation (in excess of a doubling of ambient UV-B_{BE}) did not suppress growth or seed yield of Essex, Coker 6955, or S 53-34 soybean. Furthermore, soybean growth and yield response to O_3 were not affected by enhanced UV-B radiation treatments. Measures of leaf gas exchange (NCER, g_s, and Trn) in Essex soybean were not suppressed by UV-B. On the other hand, O_3 treatment consistently induced visible injury, suppressed NCER and leaf WUE, accelerated reproductive development, and suppressed growth and yield. The results suggest that UV-B radiation up to a doubling of current ambient UV-B_{BE} levels will have little direct effect on soybean growth and yield.

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