Sulfur Dioxide Effects on Yield and Seed Quality in Field-Grown Soybeans

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ABSTRACT

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Field plots of soybeans were periodically exposed to elevated levels of sulfur dioxide (mean concentrations ranging from 0.09 to 0.79 ppm during fumigation) with an open-air fumigation system which minimized disruption of the normal crop environment. Although visible injury was observed in only two plots, yield at harvest was reduced in every fumigated plot compared to nearby unfumigated control plots. These yield decreases ranged from 5% to 48% and were somewhat greater than might have been expected from previous studies. Yield reductions seemed to be due to decreases in both the mean weight per seed and the number of seeds per plant. Harvest ratio (the ratio of bean weight to chaff weight at harvest) also was reduced in the more heavily fumigated plots. Seed quality was affected less than seed yield, although at the higher exposure levels protein content decreased slightly and concentrations of some mineral elements were altered.

Attempts to evaluate the economic impact of possible increases in sulfur dioxide (SO_2) emissions have been hampered by a lack of data relating specific air pollution levels to yield reductions at harvest in agricultural crops. For example, soybeans are a major crop throughout the world, and are known to be quite sensitive to SO_2 pollution (1), but there are no published data relating reductions in soybean yield to atmospheric SO_2 levels. Davis (7) developed a quantitative relationship between leaf damage and yield reductions by exposing plants to brief, severe fumigations, but did not indicate the levels of SO_2 required to produce specific amounts of damage. Jones et al (11) found that even when visible injury did occur there was no yield reduction when the injury occurred in the early stages of crop development. Heagle et al (9) found neither increased visible injury nor yield reductions in field-grown soybeans after 133 six-hour fumigations at 0.1 ppm SO_2. None of these studies showed what levels of SO_2 were required to cause yield reductions, or what yield reductions could be expected at given levels of SO_2 pollution in chronically impacted areas.

In the present study, an open-air fumigation system similar to the Zonal Air Pollution System developed by Lee et al (14) was used to regularly expose field-grown soybeans to elevated levels of SO_2 during two growing seasons. This fumigation system, which is described in detail elsewhere in this journal (20), permits fumigation of crops under agricultural conditions with minimal alteration of the normal crop environment and also mimics the variability in SO_2 levels normally found in polluted areas. An earlier paper (21) discussed the changes in photosynthetic rates observed during the fumigation episodes. This paper will consider the effects of the various SO_2 levels on the quantity and quality of soybeans harvested from the treated plots.

MATERIALS AND METHODS

Study area and crop. The studies were conducted on two adjacent fields of soybeans (*Glycine max* [L.] Merr. 'Wells') in Kendall County, IL, 65 km southwest of Chicago. The fields are annually rotated between corn and soybeans, so that each field had been in corn the previous year. Both fields are virtually flat, and the soil in both is a relatively uniform Martinton silt loam, which is characterized by a high organic matter content, slightly acid pH, and high water-holding capacity (26). Neither field was fertilized in the year it was studied, but each had been fertilized with nitrogen in the previous year.

The summer of 1977 had near-normal temperatures and total precipitation 45% greater than normal for the Chicago area. Most of the excess rainfall occurred in August. There were no prolonged droughts, and the plants were rarely observed to be under significant water stress. In the spring of 1978 a long wet period which delayed planting was followed by a dry period which slowed early plant development. The summer, however, was relatively normal, with temperatures 0.7 C below the average and rainfall higher than usual in July and lower than usual in August. During the fumigation period there were no periods of significant water stress.

Ambient SO_2 concentrations were monitored during all fumigations and typically ranged from 0.005 to 0.015 ppm. The study field is not near any major SO_2 sources and there is no reason to believe that significantly higher levels ever occurred in the unfumigated plots.

The fumigation system. The open-air fumigation systems used in this study consisted of pipes suspended 15–30 cm above the crop canopy, from which SO_2 diluted with ambient air was released at a controlled rate during the fumigations (Fig. 1). In 1977, three plots were fumigated, with achieved arithmetic mean concentrations of 0.12, 0.30, and 0.79 ppm and standard deviations ranging from 41% to 64% of the mean (20). A fourth plot was set up with a pipe network, but with no SO_2 release as an ambient control, to see if the pipes themselves or their installation influenced crop yield. Fumigations were begun on 13 July and continued until 29 August. The plots were fumigated 24 times during this period, for an average of 4.7 hr per fumigation. In 1978, five plots were fumigated, with mean SO_2 concentrations of 0.09, 0.10, 0.19, 0.25, and 0.36 ppm and standard deviations of 44–54% of the mean (20). Eighteen fumigations averaging 4.2 hr each were carried out between 19 July and 27 August. In both years fumigations were begun when the plants were in full bloom and pods beginning to form and continued until senescence was well underway. Although little is known about the sensitivity to SO_2 of soybean plants at different growth stages, this is the period when final yield is most sensitive to other stresses such as hail and insect defoliation (8). The fumigation system and the SO_2 levels delivered are described in greater detail elsewhere (20).

Sampling design. In 1977 four yield subplots, each four rows wide and 6.1 m long, were established near the center of each fumigation plot (Fig. 1). Preliminary monitoring showed that SO_2 levels near the distribution pipes were considerably more variable and often much higher than elsewhere in the fumigation plot, so the yield plots were centered between the pipes and crop rows directly under or adjacent to the pipes were excluded.

Because the fumigated plots were spaced fairly far apart in the field (50 m), it was thought that there might be significant soil differences among the different fumigation plots. To account for this, two control subplots were established 10–15 m west of each fumigated plot in 1977. To avoid fumigating these controls, fumigations were not applied when the wind was from the east.

In 1978, four control subplots were designated for each fumigation plot, and they were located ~3m south of the fumigated plots, somewhat closer than the 1977 plots. Fumigations were performed only when the wind was from the south, southeast, or southwest, and the two northernmost release pipes were eliminated. The fumigated yield subplots were located the same as before relative to the remaining pipes. (Fig. 1).

A soil sample composed of five plow-layer cores was taken from each fumigated and control yield subplot and analyzed for soil pH, organic matter, available P and K, exchangeable Ca and Mg, and sulfate S by the Soil and Plant Analysis Laboratory of the University of Wisconsin in Madison (15).

Plants in all of the treated and control plots were examined at least once a week during the treatment period for evidence of chlorosis, necrosis, or other visible injury due to the SO_2 treatment. The percent necrotic leaf tissue reported here was estimated approximately 2 wk before normal plant senescence.

In both years the yield subplots were harvested by rows in late September. In all subsequent statistical analyses each row was considered as a sample. Subsamples of the beans from each row were oven-dried at 70 C to constant weight to determine moisture content. Subsamples of the harvested beans were analyzed for oil and protein content by the University of Illinois Department of Agronomy (Champaign) and for the elemental content by the Soil and Plant Analysis Laboratory (Madison). In 1977, the chaff (defined here as all parts of the dried plant except the seeds) also was collected at harvest time, oven-dried, and weighed.

In addition to the row harvest, eight individual plants (10 in 1977) were randomly selected from each fumigated or control subplot at harvest and separated into stems, pods, and seeds, which were oven-dried and weighed. In statistical analyses of these data, each individual plant was treated as a sample.

The fumigated plot designated as Medium-1 in 1978 served as the control for an experiment on the interaction of SO_2 fumigation and acid rainfall (P. M. Irving, *unpublished*). For this reason some of the sampling procedures used elsewhere were not carried out in this plot and data from it are not included in some of the tables.

TABLE 1. Analyses of soils from soybean yield subplots fumigated with SO_2 in an open air fumigation system

Year and treatment level	Soil pH	Organic matter (metric tons/ha)	Available P (kg/ha)	Available K (kg/ha)	Exchangeable Ca (kg/ha)	Exchangeable Mg (kg/ha)	Sulfate-S (kg/ha)
1977							
Ambient	6.58	112	55	293	7,000	2,140	11.5
Control	6.63	118	68	339	7,250	2,180	18.0
Low	6.48	92	54	259	6,000	1,680	18.2
Control	6.48	100	62	291	5,650	1,650	15.9
Medium	6.40	86	43	252	6,200	1,790	14.4
Control	6.58	93	61	305	6,050	1,580	16.7
High	6.40	96	57	295	6,600	2,020	21.3
Control	6.48	116	59	302	6,600	1,830	20.9
1978							
Low-1	6.50	106	84	330	11,500	2,760	28.8
Control	6.68	114	78	364	15,000	3,260	28.1
Low-2	6.35	97	70	356	11,400	2,690	28.6
Control	6.20	97	69	332	10,700	2,620	33.1
Medium-1	6.40	88	77	320	10,500	2,800	22.3
Control	6.40	91	68	303	10,300	2,800	34.8
Medium-2	6.45	136	86	392	17,200	4,560	30.9
Control	6.35	143	132	430	16,300	4,190	29.2
High	6.28	118	91	386	16,300	4,200	27.4
Control	6.33	120	66	361	16,400	4,090	26.4
$LSD_{P=0.05}$	0.17	6	14	34	850	240	3.5

RESULTS

Soils. Analysis of data from the soil samples confirmed that there were significant soil differences between the fumigated plots in both years, particularly in organic matter content and exchangeable cations (Table 1). In a few cases there were also significant soil differences between fumigated plots and their respective controls. Generally, however, these were much smaller than the differences among the fumigated plots and exhibited no particular pattern; many differences appear to be due to random sampling variation. Since levels of the major nutrients in all plots were within the optimum ranges for soybean cultivation (25), it seems unlikely that the nutrient differences had any substantial effect on yield differences between fumigated and unfumigated plots.

Seed yield. Statistically significant differences in yield were detected among the unfumigated control subplots in both years, which made it inappropriate to compare the various fumigation plots with each other directly (Table 2). However, the yield in the 1977 plot with distribution pipes but no SO_2 release ("ambient-fumigated" in Table 2) was the same as that in the adjacent pipeless "ambient-control" plot, so the presence of the pipes and the disturbance involved in installing them apparently had no significant effect on yield. In view of this, and considering the proximity of the control and fumigated subplots, it is appropriate to estimate yield reductions due to fumigation by comparing each fumigated plot to its own nearby control plot.

Every plot exposed to elevated levels of SO_2 exhibited a statistically significant yield reduction compared to its control

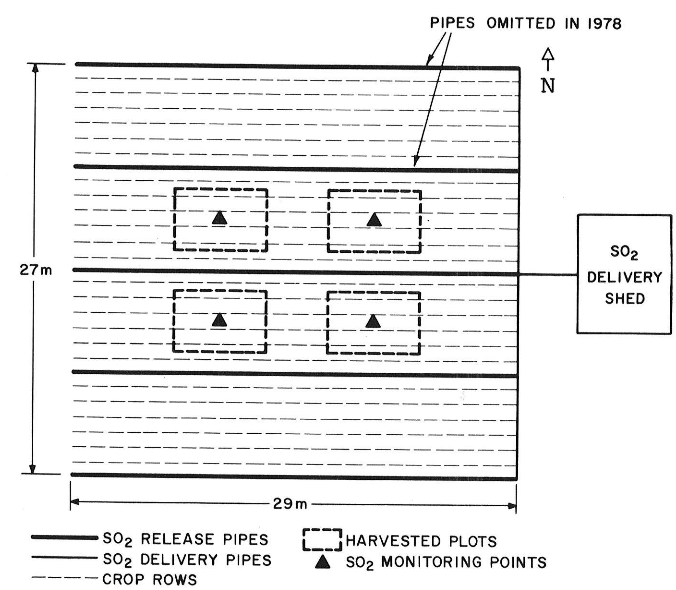

Fig. 1. Diagrammatic representation of the open-air SO_2 delivery system for field plots in which SO_2 was released from 0.08-cm holes at 0.76-m intervals in the release pipes.

(Table 2). This occured even though visible injury was observed only in the 1977 high plot (mean SO_2 concentration = 0.79 ppm), where most of the plants exhibited extensive chlorosis and some necrosis (2–5% of leaf area), and in the 1978 high plot ($\bar{x}$ = 0.36 ppm), where some of the plants were slightly to moderately chlorotic.

The sampling of individual plants at harvest time was designed to provide more detailed information on the cause of the yield reductions. However, statistically significant changes in most parameters were seen only in the 1977 high plot, where tissue damage was extensive and yield was reduced 45%. In this plot the number of filled seeds per plant was reduced by 19%, and the mean weight per filled seed was reduced 20% (Table 3). The number of pods was reduced 15%, and while the number of ovules per pod remained constant at 2.75, a higher fraction of the ovules remained unfilled, so the number of filled seeds per pod decreased slightly.

Substantial changes in yield parameters may also have occurred on the other fumigated plots, but if so, high variability among the sampled plants precluded their detection at a statistically significant level. Mean weight per seed was the only parameter which exhibited a fairly constant pattern; it was lower in all of the fumigated plots, with statistically significant reductions in all but one of the plots fumigated in 1978 and in the 1977 low and medium SO_2 plots (Table 3). The numbers of pods and seeds per plant were lower in all of the more heavily fumigated plots, but the differences were statistically significant only in the 1977 high-SO_2 plot.

Harvest ratios. In 1977, when chaff was collected at harvest time, its weight was also reduced in the medium and high plots, but the reductions were smaller than those for bean yield (Table 3). As a result, the "harvest ratio" (the ratio of seed weight to chaff weight) was also reduced significantly in the high and medium plots, indicating that the SO_2 fumigation has more effect on the economically important seed yield than on the less important vegetative tissues. Data from the individually harvested plants indicated that both pod weight and stem weight were reduced, although as with the seed parameters only the 1977 high plot exhibited statistically significant differences.

Seed quality. In both 1977 and 1978 seed quality was affected much less by the fumigation treatment than was seed yield (Table 4). In both years protein content was reduced slightly at the highest SO_2 concentration, while oil content was unchanged. (The apparent increase in oil content in the 1977 medium plot seems to have been a sampling anomaly; beans from the fumigated plots were in the same range as those from all the other plots, but the oil content of beans from the medium-SO_2 control plot was exceptionally low.)

Concentrations of the major fertilizer elements (N, P, and K) in the beans were not affected by the fumigation treatment. Total sulfur content of the beans increased in most of the fumigated plots, although the increase was statistically significant only in the medium and high plots in 1977 and in one of the low plots in 1978. Increases in sulfur content of the beans were much smaller than increases in sulfur content in leaves of the exposed plants (authors', *unpublished*) indicating that little of the extra sulfur incorporated into fumigated leaves from the air is translocated to the seeds. Magnesium and boron concentrations were down 5 – 10% in the medium and high plots in both years, while zinc concentrations increased by about the same fraction in the high plots in both years. Copper, manganese, and calcium concentrations all increased in the high plot in 1977, but showed no consistent pattern elsewhere. None of the other macro- or micronutrient elements exhibited a consistent pattern of change under the fumigation treatment.

TABLE 2. Yield reductions in soybeans subjected to varying concentrations of SO_2 in an open-air fumigation system, 1977–1978

Plot	Mean SO_2 concentration (ppm)	"Dose" (ppm-hr)	Yield (kg/ha)		Yield reduction (%)
			Fumigated plot	Control plot	
1977					
Ambient	0.005–0.015	...	2,566 ± 77[a]	2,577 ± 73[a]	0.3 ± 4.2[a]
Low	0.12	13.3	3,052 ± 92	3,478 ± 101	12.3 ± 4.3 ($P<.01$)[b]
Medium	0.30	34.2	2,482 ± 65	3,140 ± 48	20.5 ± 3.1 ($P<.001$)
High[c]	0.79[d]	89.6	1,636 ± 52	2,992 ± 120	45.3 ± 3.7 ($P<.001$)
1978					
Low 1	0.09	6.8	2,370 ± 27	2,531 ± 47	6.4 ± 2.1 ($P<.01$)
Low 2	0.10	7.8	2,256 ± 40	2,379 ± 43	5.2 ± 2.5 ($P<.05$)
Medium 1	0.19	13.5	2,191 ± 65	2,492 ± 41	12.2 ± 3.1 ($P<.001$)
Medium 2	0.25	18.9	2,008 ± 27	2,485 ± 42	19.2 ± 2.0 ($P<.001$)
High[c]	0.36[d]	26.1	1,859 ± 48	2,209 ± 45	15.9 ± 3.0 ($P<.001$)

[a]Values are given ± standard error.
[b]Significant yield reductions determined by *t*-test.
[c]Visible injury observed on fumigated plants.
[d]Exceeded U.S. Environmental Protection Agency Secondary Air Quality Standards for sulfur oxides.

TABLE 3. Changes in soybean vegetative and reproductive parameters in field-grown, SO_2-fumigated plants in 1977 and 1978

Parameter	Percent difference from unfumigated controls in indicated treatments: year/plot/mean SO_2 concentration (ppm)						
	1977			1978			
	Low (0.12)	Medium (0.30)	High (0.79)	Low-1 (0.09)	Low-2 (0.10)	Medium-2 (0.25)	High (0.36)
Stem weight	−1.2	−1.6	−17***[a]	−0.7	+16	−3.4	+7.7
Number of pods/plant	+1.7	−5.7	−15**	+0.4	+12	−6.8	−1.5
Pod weight (excluding seeds)	+3.4	−5.4	−22***	+0.6	+11	−8.7	+0.2
Ovules/pod	−0.4	+0.6	+1.3	−2.7	−2.9	+2.3	+1.7
Filled seeds/pod	+1.2	−2.4	−5.4**	−2.0	−0.7	+1.0	+0.2
Filled seeds/plant	+3.0	−7.4	−19***	−2.8	+11	−5.9	−1.0
Mean weight/filled seed	−5.2	−2.9	−20***	−1.0	−7.5**	−13***	−7.6**
Chaff weight	−2.5	−7.5*	−24***	(n.d.)[b]	(n.d.)	(n.d.)	(n.d.)
Harvest ratio	−10	−15**	−28***	(n.d.)	(n.d.)	(n.d.)	(n.d.)

[a]*, **, and *** indicate statistically significant difference at $P<0.05$, $P=0.01$, and $P=0.001$, respectively.
[b]n.d. = not determined.

DISCUSSION

Quantitative prediction of yield reductions. Generally speaking, the amount of yield reduction by a series of air pollution episodes is determined by both the pollutant concentration and the duration of the exposures (modified, of course by environmental conditions, stage of crop development, cultivar sensitivity, etc.). For this reason, time and concentration often are multiplied to give an estimate of "dose." Where high concentrations are reached, this estimate of "dose" is not adequate to predict yield reduction, since short exposures (1–2 hr) to very high pollution levels (>2 ppm) may cause tissue necrosis or other permanent injury which might not occur if the same dose were administered over a longer period of time. However, at pollution levels where visible injury does not occur, dose may be a useful predictor of yield reduction. Further studies of this question, including exposure of field-grown plants to a single concentration of SO_2 for varying lengths of time, are being conducted.

For combined 1977 and 1978 data, the second-order polynomial which best expressed the relationship between yield and SO_2 dose was

$$y = 100 - 0.803\,x + 0.0034\,x^2 \quad (r^2 = 0.948)$$

in which y is the yield (expressed as percent of the control) and x is dose in ppm-hr. However, the exponential equation

$$y = 100 \cdot e^{-0.0072\,x} \quad (r^2 = 0.934)$$

gave nearly as good a fit to the data and is much more realistic mechanistically (Fig. 2). For this set of data, dose was closely related to mean concentration during fumigation since in each year all the plots were fumigated for the same length of time and total fumigation time did not differ greatly between 1977 and 1978. Thus, it is not surprising that mean concentration during fumigation was also a good predictor of yield reduction for this data set. The best prediction equation was

$$y = 100 \cdot e^{-0.71\,x} \quad (r^2 = 0.933)$$

in which y is as above and x is mean concentration in parts per million (Fig. 3). No polynomial relationship was significantly better than this exponential relationship.

Comparison with previous studies and general discussion. The results of this study differ in several ways from previous studies of the effect of SO_2 on soybeans and other crop plants. Heagle et al (9) found no yield reductions in cultivar Dare soybeans after 133 six-hour fumigations at 0.10 ppm, in contrast to 5–12% yield reductions in our low plots after 18–24 four- to five-hour fumigations at concentrations averaging 0.09–0.12 ppm. It is difficult to compare the two studies, since in addition to the difference in soybean cultivar, we used an open-air system while they used closed field chambers which may have modified the microenvironment of the treated plants and affected their susceptibility to the pollutant. It is also possible that the yield reductions in our study resulted from the occasional high peaks (up to 0.8 ppm for one 2-min sample in 1977) rather than from the lower general mean. Such peaks are found in air pollution episodes, particularly near point sources but do not normally occur in chamber studies where the SO_2 concentration is closely controlled.

A third possibility is that synergistic interactions with ozone (O_3) may have increased the effects of SO_2 in our study. Ozone levels in

TABLE 4. Oil, protein, and elemental concentrations in seeds from soybean plants fumigated with varying levels of SO_2 and in nearby unfumigated controls

Component	Concentration in fumigated beans and (control) in indicated treatment: year/plot/mean SO_2 concentration (ppm)						
	1977			1978			
	Low (0.12)	Medium (0.30)	High (0.79)	Low-1 (0.09)	Low-2 (0.10)	Medium-2 (0.25)	High (0.36)
Protein (%)	40.5 (40.2)	40.1 (40.8)	38.4 (39.6)**[a]	43.1 (43.0)	43.5 (43.1)	44.1 (43.9)	43.8 (44.5)**
Oil (%)	21.5 (21.3)	21.5 (20.8)**	21.5 (21.5)	18.8 (19.2)	19.1 (19.7)	19.0 (18.4)	19.0 (19.0)
Nitrogen (%)	6.62 (6.57)	6.59 (6.74)	6.30 (6.48)	6.44 (6.45)	6.84 (6.84)	6.68 (6.78)	6.79 (7.00)
Phosphorus (%)	.536 (.538)	.544 (.551)	.550 (.547)	.597 (.592)	.611 (.600)	.597 (.603)	.594 (.595)
Potassium (%)	2.05 (2.01)	2.03 (2.01)	2.14 (2.09)	1.95 (1.98)	1.92 (1.82)	1.78 (1.91)	2.07 (2.02)
Sulfur (%)	.328 (.340)	.393 (.353)***	.446 (.350)***	.361 (.304)**	.310 (.305)	.341 (.303)	.393 (.344)
Calcium (%)	.192 (.200)	.193 (.200)	.204 (.191)**	.221 (.214)	.213 (.199)***	.216 (.219)	.212 (.212)
Magnesium (%)	.242 (.252)	.235 (.253)**	.233 (.252)***	.257 (.258)	.264 (.257)	.241 (.260)***	.237(.250)***
Copper (ppm)	9.6 (9.4)	10.0 (9.3)	12.5 (9.6)**	11.1 (12.2)	9.5 (10.7)	10.9 (11.6)	11.7 (11.8)
Zinc (ppm)	40.2 (38.7)	42.3 (41.0)	44.9 (40.3)***	45.6 (43.5)	48.0 (46.1)	46.4 (44.4)	43.9 (41.0)**
Manganese (ppm)	18.4 (18.1)	20.6 (20.5)	18.0 (20.4)**	24.1 (22.2)**	26.4 (24.7)	22.6 (22.6)	22.2 (22.2)
Boron (ppm)	29.0 (30.6)	27.7 (30.3)***	27.6 (29.5)**	28.7 (30.4)**	28.9 (30.0)	27.6 (31.0)***	26.9 (29.1)***

[a] ** and *** indicate differences significant at $P < 0.01$ and $P = 0.001$, respectively.

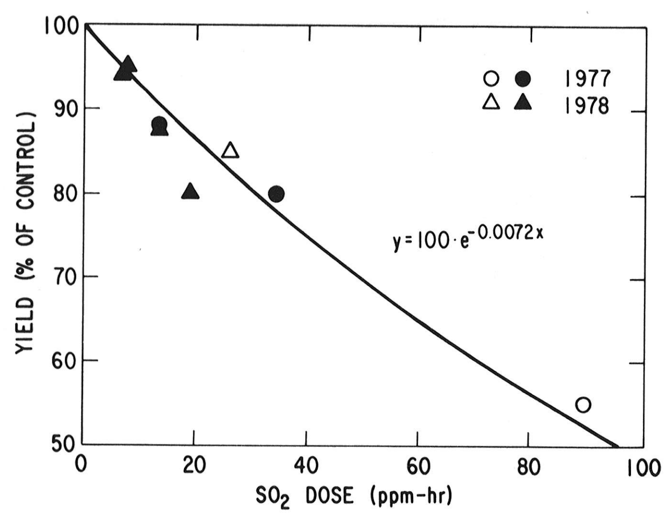

Fig. 2. Relation between SO_2 "dose" (concentration × time) and yield of soybeans in field plots fumigated with an open-air delivery system. Open symbols indicate plots in which visible injury was observed.

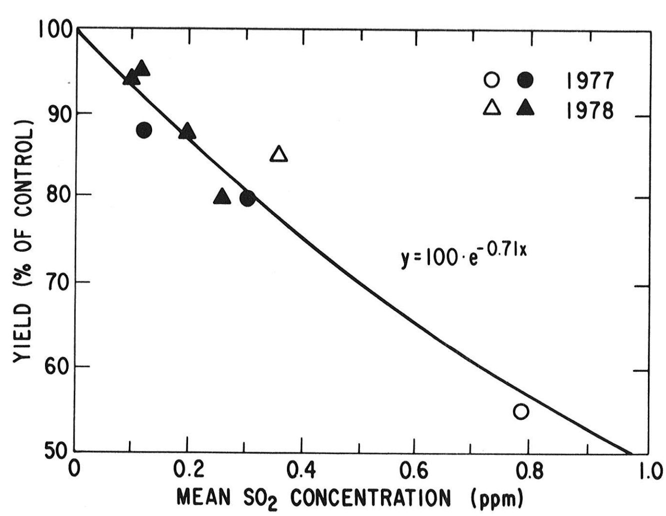

Fig. 3. Relation between mean SO_2 concentration and yield of soybeans in field plots fumigated with an open-air delivery system. Open symbols indicate plots in which visible injury was observed.

the study field were monitored during the first part of the 1977 field season, and generally averaged 0.05 to 0.06 ppm during the fumigations, but on at least two occasions exceeded 0.1 ppm for 1 hr or more. Ozone data were not available for the 1978 season, but data from nearby Joliet, IL, suggest that ozone levels were similar to 1977. Several authors have observed an SO_2/O_3 synergism on Bel-W3 tobacco (10,19). However, recent studies on soybeans (9) and red kidney and Tempo beans (10) produced no evidence for greater-than-additive effects.

A more important difference between our results and those of previously published studies is that significant reductions in harvest yield were observed without any visible injury. In a previous study on soybeans (7) and several studies of other crop plants (4,5,13) reductions in final yield were found only when foliar injury was present. However, in many of these studies, one or two intense fumigations were used rather than the repeated milder exposures which we employed. Several other recent studies using low-level fumigations have shown growth reductions in crop plants without visible injury, although these studies have dealt only with vegetative growth and not with final harvest yield of grain crops or legumes (2,3,16,23). Reductions in photosynthetic rate can certainly occur in the absence of visible injury (6,27); for example, in our medium plot in 1977 photosynthesis was reduced by 15 – 35% during fumigation compared to nearby unfumigated plants (21). In the high plot, where injury often was severe, photosynthesis was reduced 35–65% during fumigation. In the low plot photosynthetic reduction was never observed, and in fact on one occasion a 37% increase in the photosynthetic rate was noted. If SO_2 levels sufficient to depress photosynthesis occur frequently enough, yield reductions must almost inevitably result. While it may never be possible to detect yield reductions due to a single SO_2 episode which does not result in visible damage to leaves, the additive effects of repeated moderate fumigations may ultimately be more significant than a single episode which causes some visible injury, but does not result in the loss of large percentages of photosynthetic tissue.

Our data suggest, moreover, that other factors may be even more important than photosynthetic inhibition in reducing final yield at low SO_2 levels. The best evidence for this is that there were yield reductions in the low plots in both years, even though SO_2 concentrations rarely if ever reached the levels at which Muller et al (21) found significant photosynthetic reductions. Even in the more heavily fumigated plots, where photosynthesis was depressed during the fumigations, the yield decreases were larger than would have been expected from photosynthetic reduction alone. For example, in the 1977 medium plot, simple calculations suggest that the SO_2-induced reduction in gross photosynthesis should have been less than 5% of the total production during the treatment period. Since the actual yield reduction was 20%, inhibition of photosynthesis can account directly for only about one quarter of the total yield decrease.

There are, of course, a number of physiological processes other than photosynthetic carbon fixation which might be affected by low-level SO_2 fumigation and which might cumulatively reduce final yield. For example, if respiration or photorespiration were increased, then net photosynthesis might be reduced even if gross photosynthesis were not affected. SO_2 is known to interfere with glycolate oxidation and oxidative phosphorylation (18) and may also affect translocation of carbohydrates (22). It has been suggested that SO_2 may damage membranes (17), so that energy would have to be expended in repair processes. Any or all of these mechanisms could be involved in causing a productivity reduction beyond that which is directly explainable by reduced gross photosynthesis.

These findings have some potentially important economic implications. Current secondary air quality standards are designed to prevent conditions which are known to cause visible injury to vegetation (12,24). However, if economically significant yield reductions can occur in the absence of visible injury, then the standards may not be adequate to prevent yield reductions in areas of chronic SO_2 pollution. More field research is clearly needed to develop appropriate yield-based evidence on which to base air quality criteria for moderately polluted areas.

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