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IMPACT OF OZONE ON WINTER WHEAT YIELD*

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KRESS L. W., MILLER J. E. and SMITH H. J. *Impact of ozone on winter wheat yield.* ENVIRONMENTAL AND EXPERIMENTAL BOTANY **25,** 211–228, 1985.—Wheat (*Triticum aestivum* L.) is one of the more important agricultural crops in the U.S.A., and the major production areas may be subjected to potentially damaging concentrations of ozone (O_3). Since no information was available regarding the O_3 sensitivity of winter wheat cultivars grown in the Midwest, plants of three cultivars ('Abe', 'Arthur-71', and 'Roland') were field-grown in open-top chambers and exposed to O_3 daily throughout the spring growing season to determine impact on grain yield. All three cultivars were exposed to 7-hr/day seasonal mean O_3 concentrations of 0.023, 0.041, 0.068, 0.095 and 0.122 ppm for 55 days in 1982, and two cultivars ('Abe' and 'Arthur-71') were exposed to 0.018, 0.044, 0.062, 0.078 and 0.095 ppm O_3 for 53 days in 1983. The air in the chambers was either charcoal-filtered or nonfiltered with various constant amounts of O_3 added to the ambient O_3 (seasonal means of 0.042 ppm in 1982 and 0.045 ppm in 1983). Also included was a non-chambered ambient air plot. A split-plot randomized complete block design incorporated six O_3 treatments and four replications in 1982 and three replications in 1983. Split-plot analysis of covariance (using number of heads/m as the covariate) indicated significant ($P = 0.05$) O_3, cultivar, $O_3 \times$ replication, and $O_3 \times$ cultivar effects in 1982, but only significant O_3 and cultivar effects in 1983. As the concentration of O_3 increased, there was a general decrease in all yield variables in 1982, but only the weight yield variables in 1983. About one-third of the overall grain yield reductions in 1982 were accounted for by reduction in seed number/m, but in 1983 seed number/m was not reduced. 'Roland' was significantly ($P = 0.05$) more sensitive to O_3 than 'Abe' and 'Arthur-71'. There also were indications of significantly ($P = 0.05$) greater sensitivity to O_3 in 1982 vs 1983. Exposure-response models were developed for 'Roland', 'Abe' + 'Arthur-71' in each year, and for the combined 1982 + 1983 'Abe' + 'Arthur-71' data.

INTRODUCTION

WHEAT has been among the top four U.S.A. crops in terms of acreage planted and dollar value since 1960. It accounts for about 11% of the total cash value of U.S.A. crops, and 51% of that value is generated in six states: Kansas (17%), N. Dakota (9%), Oklahoma (8%), Washington (7%), Montana (5%) and Texas (5%).[14]

Although data for pollutant concentrations are limited in many of the areas where crops are grown, research and field observations suggest that ozone (O_3) may be responsible for up to 90% of all crop loss in the U.S.A. caused by air pollution.[2,5,11] The available air quality monitoring data suggest that elevated O_3 concentrations may occasionally occur in much of the Midwest where wheat is of major import-

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ance.[1,12,15] Mean growing season O_3 concentrations ranging from 0.04 to 0.06 ppm (seasonal 7-hr/day mean, 0900–1600 ST) occur over most of these regions. (Subsequently, all O_3 concentrations referred to in this paper will be the 7-hr/day mean for the growth period of the plants unless otherwise noted.) A growing season mean concentration of 0.05 ppm O_3 has been estimated to reduce the yields of soybean, 13.4%; field corn, 1.6%; wheat, 2.3%; cotton, 11%; kidney bean, 3.1%; peanut, 12.6%; lettuce, 22.2%; turnip, 14.1%; and spinach, 9.2%.[6]

Previous work with four cultivars of soft red winter wheat (Blueboy II, Coker 47-27, Holly and Oasis) exposed to O_3 in open-top chambers indicated that yields were reduced from 1 to 11% at 0.06 ppm O_3 (seasonal 7-hr/day mean) and 11 to 25% at 0.10 ppm O_3 compared to a 0.03 ppm control treatment.[4] A comparison of the yield responses to O_3 of the four cultivars showed that the responses were homogeneous and a common response model could be used to describe them.[6]

Given the importance of winter wheat and the absence of information on the O_3 sensitivity of midwestern cultivars, there is an obvious need for more data on O_3 impacts to winter wheat yield. The study reported herein is a portion of the research at Argonne National Laboratory (Argonne, IL) as a member of the National Crop Loss Assessment Network (NCLAN) in 1982 and 1983. The study was initiated to provide further biological response data suitable for evaluating ambient air quality standards and for use in the NCLAN economic assessment of the consequences of O_3 exposure to crops. The specific objective was to establish the exposure–response relationships between yield of three important cultivars of soft red winter wheat grown in the Midwest and chronic exposures to a range of O_3 concentrations.

MATERIALS AND METHODS

Most of the methods and procedures of exposing plants to air pollution in the field have been standardized among the cooperating NCLAN scientists.[5,6] The site of this research is located approximately 40 km southwest of Chicago, Illinois, at Argonne National Laboratory. The research plot was used for field corn production in 1981, soybean production in 1980, and was in undisturbed turf for at least 20 years prior to 1980. The soil is a Morely silt loam (fine, illitic, mesic, Typic Hapludalf), upland timber soil, with a high water holding capacity and low permeability. The study was performed over two seasons with some differences in experimental design, so each year will be described separately.

1982

Three cultivars of soft red winter wheat (*Triticum aestivum* L., 'Abe', 'Arthur-71', 'Roland') were planted in alternating rows on a 20.3 cm row spacing with a grain drill at a predicted rate of 90 kg/ha on 13 October 1981. An area of the research plot with a pH of 5.95 ± 0.24 and 34,000 ± 5000 kg/ha organic matter was fertilized with 40 kg/ha N and 103 kg/ha P (18-46-0) in early October 1981. The following spring (11 April 1982), the plot was fertilized with N (50 kg/ha as NH_4/NO_3). Soil test results following the 1982 season indicated 43 ± 22 kg/ha P and 209 ± 45 kg/ha K, and no significant plot-to-plot variability. Irrigation was not necessary due to slightly above normal rainfall (18.6 cm between 1 May and 3 July 1982). The plots were hand weeded as necessary, and no pesticides were used as disease problems were minimal.

Open-top chambers 3 m diameter by 2.43 m high[3,5] were established over 20 experimental plots on 7 May. The O_3 treatments began on 8 May shortly after the plants had begun their spring growth and were about 15 cm tall, and were terminated on 2 July when the plants in all treatments had brown leaves, stems and heads.

The experiment consisted of a split-plot experimental design with the whole plot treatments (O_3 levels) arranged in a randomized complete block design with four replications. The six whole plot treatments were: AA, no chamber; CF, charcoal-filtered air chamber; NF, nonfiltered air chamber with a small amount of O_3 added to provide a concentration equal to that in the ambient air (a small amount of O_3 is lost as the ambient air passes through the particle filter, fan and chamber assemblies); and NF + 0.03, NF + 0.06 and NF + 0.09, nonfiltered air plus approximately 0.03, 0.06 and 0.09 ppm O_3 above ambient, respectively. The subplot treatments were the three wheat cultivars 'Abe', 'Arthur-71' and

'Roland'. These treatments thus encompassed a wide range of conditions ranging from relatively O_3-free to highly O_3-polluted.

Ozone generation and monitoring has been described in detail previously.[9] All O_3 sampling lines (6.35 mm diameter FEP Teflon) were of uniform length and their efficiencies in transmitting O_3 were checked before, during and after the experiment. Sampling line losses of 5–7% were noted and concentration measures were corrected. Bendix* chemiluminescent O_3 monitors (Combustion Engineering, Lewisburg, WV) were calibrated with a Columbia Scientific Industries Photocal 3000 (Columbia Scientific Industries, Austin, TX) several times per week, and an independent audit during the experiment verified correct instrument operation. Two O_3 monitors each sampled 10 chambers and one open plot on a 2 min/plot time share system. Thus, each chamber and two open plots were sampled for two out of every 22 min (only the last minute of each reading was used in concentration calculations). All O_3 sampling inlets were maintained at canopy height. A third O_3 monitor sampled ambient O_3 continuously at a 6 m height. During each day, the proper functioning of the instruments was checked by comparing the ambient air readings of all three monitors.

Ozone was added to the chambers from 0900 to 1600 CST daily, since plants are most active metabolically and O_3 concentrations are usually highest during that time period. The chamber fans were turned off nightly (2130–0530) to allow dew formation and minimize the chamber effect. Since ambient O_3 concentrations are generally low during extended rainy periods, fumigations were not made then. Decisions were made twice daily (0900 and 1230 CST) whether or not to initiate the O_3 addition treatments. The combination of rain and completely overcast skies dictated that the O_3 treatments not be started. Out of 56 possible fumigation days, exposures on two full days and five half-days were cancelled due to rain (but the O_3 concentrations were still recorded and included in the seasonal means).

Ambient SO_2 was monitored with a TECO Model 43 Pulsed Fluorescent SO_2 analyzer and a Meloy SA285 Flame Photometric sulfur analyzer. Zero and span checks were made weekly and multipoint calibrations were performed monthly with a Columbia Scientific Industries 1700 Gas Phase Titration Calibrator and a calibrated SO_2 bottle.

One 2-m row section of each cultivar was harvested from the center of each plot on 6–12 July. The grain was hand threshed and cleaned, oven dried to < 1% moisture content (to assure that sample differences were not confounded by differing moisture content) and weighed on a calibrated balance. Measurements taken at harvest were number of heads/m and plant height. Seed weight per 1 m of row was adjusted to reflect 14% moisture content and converted to kg/ha. The weight of 100 seeds (100-seed wt) was also obtained for each plot. The number of seeds/m was calculated by dividing the seed wt/m by the 100-seed wt and multiplying by 100. Soil samples were collected from each plot following plant harvest. Five, 10 in.-deep cores were pooled from each plot. Analyses for pH, OM, P and K were performed by the Soil and Plant Analysis Laboratory, University of Wisconsin-Extension.

A split-plot analysis of variance was performed on the chamber plot data for grain yield (kg/ha), 100-seed wt, seed weight per head, number of seeds per head, number of seeds per meter row, number of heads per meter row, and plant height. The differences in number of heads per meter row were assumed to be unrelated to the O_3 treatments (the shoots on which heads developed were elongating prior to treatment), and a split-plot analysis of covariance was performed for grain yield and number of seeds/m using the number of heads/m as a covariate. Analyses of variance and covariance were also performed for each cultivar.

A *t*-test was used to test for significant differences in plant yields between the AA and NF treatments to evaluate the "chamber effect". Weibull response models were developed for grain yield for each cultivar and the combined cultivars utilizing the SAS† nonlinear procedure (PROC NLIN) (SAS Institute, Inc., 1982). The Weibull

* Any mention of a trademark or proprietary product does not imply approval or recommendation of these products by Argonne National Laboratory or sponsors to the exclusion of other products that may be suitable.

† SAS is a registered trademark of SAS Institute, Inc., Cary, NC.

response model, taken from the Weibull cumulative probability distribution function, provides a convenient mathematical form for the yield ozone exposure–response models. The model is given as

$$\text{yield} = \boldsymbol{\alpha} \cdot \exp\left[-(O_3/\boldsymbol{\sigma})^c\right], \qquad (1)$$

where α is the yield at 0.00 ppm O_3, O_3 is the 7-hr/day seasonal mean ozone concentration in ppm, σ is the O_3 concentration in ppm at which yield is reduced to 0.37 α, and c is a dimensionless parameter controlling the shape of the yield loss curve. The exponential part of the model measures the proportion of the yield remaining. The homogeneity of the responses to O_3 of the three cultivars was tested by considering three types of Weibull models (J. O. Rawlings and W. W. Cure, unpublished data. The 'simple' Weibull requires the same yield level and proportional response to O_3 for all cultivars. The 'common' Weibull allows different yield levels for the cultivars, but requires the same proportional response to O_3. The 'full' Weibull allows each cultivar to have its own yield level and response to O_3. The responses to O_3 are considered homogeneous if the 'full' Weibull is not a significant improvement over the 'common' Weibull.

1983

Only two of the cultivars tested in 1982 ('Abe' and 'Arthur-71') were tested again in 1983, because of a desire to obtain a larger sample size for each cultivar and because 'Roland' is considerably less widely planted than the other two. Another area of the research plot was used, with a pH of 6.1 ± 0.4 and 47,000 ± 9000 kg/ha organic matter. In the spring of 1982, this part of the field had received 112 kg/ha and was planted with alfalfa. The alfalfa was plowed under in September and the field received 20 kg/ha N, 80 kg/ha P and 80 kg/ha K. (Soil test results following the 1983 season indicated 35 ± 8 kg/ha P and 202 ± 28 kg/ha K, and no significant plot-to-plot variation.) Seed of the two cultivars was hand-sown (because of a suspected problem with the accuracy and uniformity of the grain drill used in 1982) at a predicted rate of 40 seeds/m in 2.7 × 3.5 m plots in October 1982. Eight 3.5 cm rows of 'Abe' were spaced 18 cm apart on the east half of each plot and eight rows of 'Arthur-71' were on the west half. In May 1983, the plots were top-dressed with 45 kg/ha N. Irrigation was not necessary due to excessive rainfall in May and June (25.8 cm) and pesticides were not used.

The chambers were established over the plots on 6 May. The O_3 treatments began on 8 May when the plants were in the 3–4 leaf stage (20–40 cm tall) and were terminated on 30 June when the plants in all treatments had brown leaves, stems and heads.

The experiment consisted of a split-plot experimental design as in 1982, except that there were only three replications, the O_3 additions were 0.02, 0.04 and 0.06 ppm, and the subplot treatments were the two cultivars 'Abe' and 'Arthur-71'.

Methods for O_3 dispensing and monitoring were as described for 1982 except that each of two O_3 monitors sampled 8 plots and thus each chamber and one open plot were sampled for 2 out of every 16 min. Sample line losses of 5% were noted and O_3 concentration values were corrected. Ozone was not dispensed on three full and five half-days due to rain. Ambient SO_2 was monitored in June with the TECO Model 43 Pulsed Fluorescent SO_2 analyzer.

Foliar injury was estimated for all treatments in one replication on 24 June. Four randomly selected flag leaves/cultivar in each plot were evaluated for percent chlorosis, stipple and necrosis. The injury on each leaf was recorded in 5% increments between 0 and 20%, and in 10% increments above 20%.

Two 2-m row sections of each cultivar were harvested from each plot on 5–9 July. Both grain and stems were collected, dried and weighed as in 1982.

Data analysis proceeded as in 1982, except that GLM was used to correct for imbalance caused by the loss of data from three treatments in one replication due to severe lodging which occurred just after heading. Weibull regression models were also developed for each cultivar, the combined cultivars, and the combined 1982 and 1983 data sets.

RESULTS

Pollutant concentrations

The 7-hr/day seasonal mean O_3 concentrations across the six experimental treatments in 1982 ranged from 0.023 ppm (CF) to 0.122 ppm (NF +0.09), and in 1983 ranged from 0.018 ppm (CF) to 0.095 ppm (NF+0.06) (Table 1). Since the O_3 exposures are not fully described by the 7-hr/day seasonal statistic alone, the O_3 concentrations have also been expressed in several ways that allow a more detailed evaluation of the exposure regimes. The highest and second highest hourly and 7-hr mean values and the seasonal daily peak 1- and 7-hr means provide information regarding peak to mean ratios for each treatment. While the mean O_3 concentration values were similar (for AA, NF and NF+0.06) for 1982 and 1983, the peak values were higher (by 6–19%) in 1983. The CF chambers were effective in excluding about 45% of the ambient O_3 in 1982, but about 60% of the ambient O_3 in 1983. The seasonal mean of the daily 1-hr peaks was about 20–25% higher than the 7-hr seasonal mean for all treatments except the CF (which was 35–40% higher) in both years. The National Ambient Air Quality Standard (NAAQS) for O_3 (0.12 ppm hourly average not to be exceeded more than once per year) was not violated in the AA, CF, or NF treatments in either year, but was violated in all NF+O_3 treatments in both years.

Concentrations of O_3 in the ambient air from 3 May to 15 July of both years are summarized as daily 7-hr (0900–1600 CST) and 24-hr means (Fig. 1). The highest 7- and 24-hr means, respectively, were 0.088 ppm (27 June) and 0.056 ppm (14 May) in 1982 and 0.098 ppm (25 June) and 0.064 ppm (13 June) in 1983. The average 1982 O_3 concentrations were higher in May than in June, but in 1983 the average O_3 was higher in June.

The diurnal pattern of the mean hourly O_3 concentration values for the six experimental treatments for each season is presented in Fig. 2. The curves appear smooth because they are seasonal mean values. The concentrations actually varied from day-to-day depending upon the

Table 1. *Highest and second highest hourly* (*within the* 0900–1600 *CST timeframe*) *and* 7-hr *mean* O_3 *values, the seasonal daily peak* 1-hr *mean, and the seasonal* 7-hr *mean for each treatment in* 1982 *and* 1983

Treatment*	1982 7-hr/day values (ppm)			1982 1-hr/day peak values (ppm)		
	Seasonal mean	Highest	2nd highest	Seasonal mean	Highest	2nd highest
AA	0.042	0.084	0.072	0.051	0.113	0.095
CF	0.023	0.045	0.044	0.031	0.082	0.060
NF	0.041	0.083	0.080	0.051	0.120	0.102
NF+0.03	0.068	0.115	0.114	0.083	0.149	0.134
NF+0.06	0.095	0.148	0.139	0.115	0.170	0.169
NF+0.09	0.122	0.180	0.173	0.149	0.220	0.210
	1983 7-hr/day values (ppm)			1983 1-hr/day peak values (ppm)		
AA	0.045	0.098	0.092	0.053	0.116 (0.135)†	0.114
CF	0.018	0.060	0.043	0.025	0.071 (0.097)	0.066
NF	0.044	0.099	0.097	0.053	0.121 (0.130)	0.119
NF+0.02	0.062	0.122	0.119	0.075	0.145	0.144
NF+0.04	0.078	0.141	0.141	0.094	0.166	0.165
NF+0.06	0.095	0.157	0.156	0.166	0.186	0.180

* Each 1982 value was calculated from three (occasionally two) 2-min samples per hour. The mean 1- and 7-hr values are averages of four replicates. Each 1983 value was calculated from four (occasionally three) 2-min samples per hour. The mean 1- and 7-hr values are averages of three replicates.

† Highest hourly value occurred outside the 0900–1600 CST timeframe.

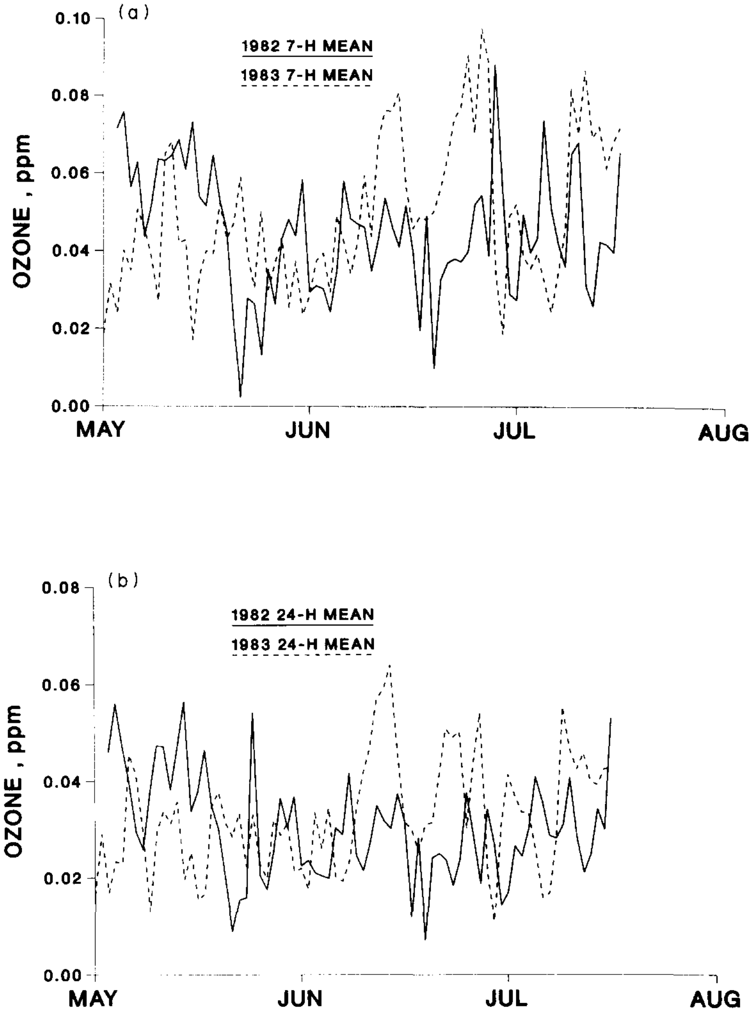

FIG. 1. Ambient O_3 data collected from 3 May to 15 July 1982 and from 1 May to 15 July 1983 showing a daily 7-hr mean (0900–1600 CST) and (b) daily 24-hr mean. In 1982, heading began on 19 May and flowering began on 28 May. In 1983, heading began on 27 May and flowering began on 9 June.

ambient O_3 concentration (Fig. 1). The O_3 in the CF treatment decreased below ambient when the chamber fans were operating. All chamber treatments generally tracked the ambient pattern during the 7-hr exposure period.

In 1982, SO_2 was detected during about 50% of the hours in May and June. The highest 24-, 3-, 1-hr means, and instantaneous values were 0.018, 0.059, 0.085 and 0.210 ppm, respectively. The 2-month values were 0.006 ppm (24-hr mean), 0.018 ppm (3-hr peak mean), and 0.026 ppm (1-hr peak mean). In 1983, SO_2 was detected during 30% of the hours in June. The highest 24-, 3-, 1-hr means, and instantaneous values were 0.018, 0.063, 0.120, and 0.180 ppm, respectively. The monthly values were 0.005 ppm (24-hr mean),

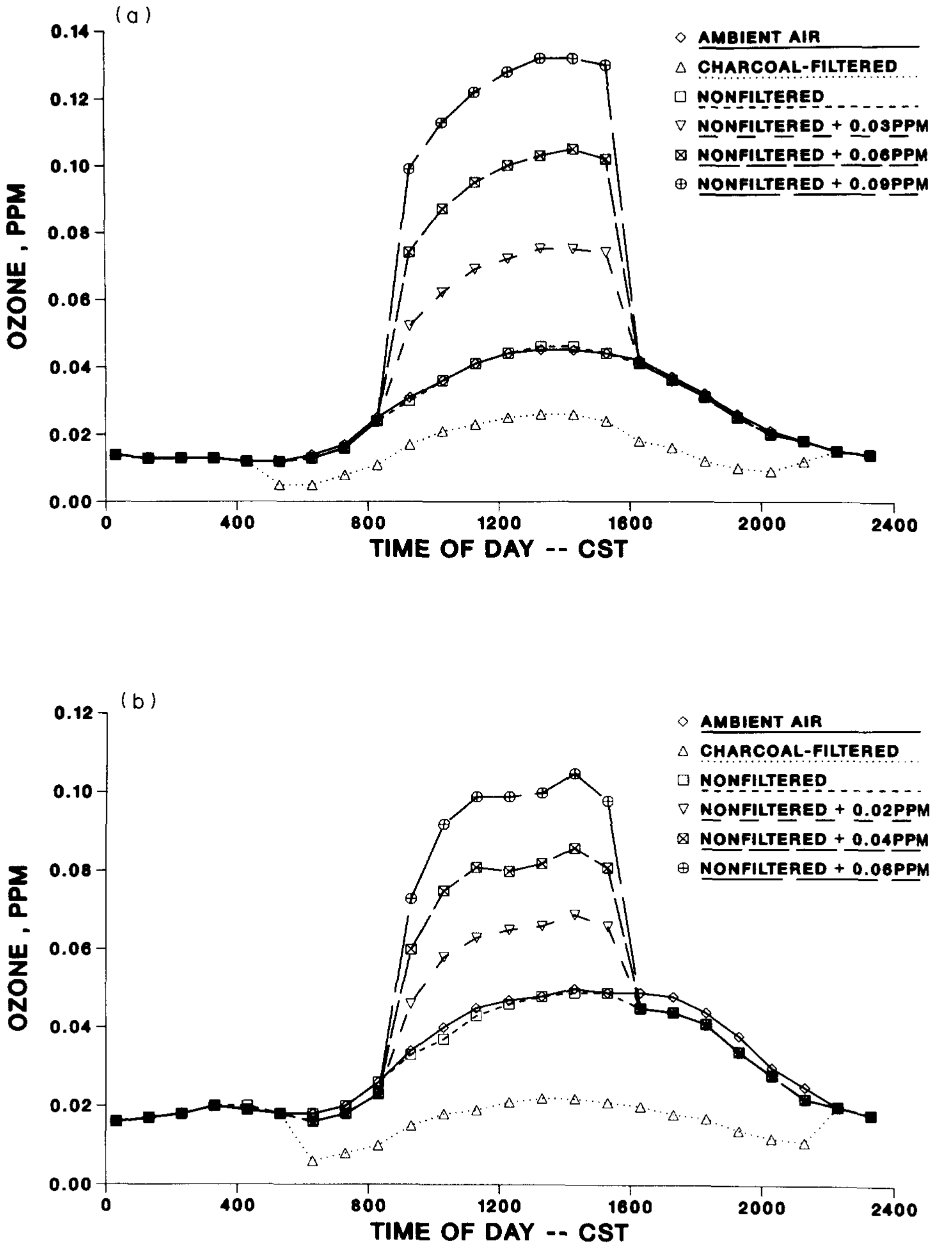

FIG. 2. Mean hourly O_3 concentrations in ambient air (AA), charcoal-filtered air chambers (CF), or in non-filtered chambers with various amounts of O_3 added from 0900 to 1600 CST. All chamber fans were turned off nightly from 2130 to 0530 CST. (a) 1982 treatments: 8 May–2 July. (b) 1983 treatments: 8 May–30 June.

Table 2. Plant height, number of heads/m, and mean percent foliar injury of two cultivars of winter wheat exposed to selected O_3 treatments in open-top chambers for 53 days in 1983

		Abe				Arthur-71			
Treatment	O_3* (ppm)	Height (cm)	Number of heads/m	Chlorosis† and stipple	Necrosis	Height (cm)	Number of heads/m	Chlorosis and stipple	Necrosis
AA	0.045	106	143	8	5	108	161	10	5
CF	0.018	106	167	8	1	108	160	11	4
NF	0.044	105	196	6	5	108	143	13	5
NF+0.02	0.062	102	154	15	4	102	137	34	5
NF+0.04	0.078	103	160	51	5	105	157	38	30
NF+0.06	0.095	96	155	80	6	100	136	58	26

* Seasonal 7-hr/day mean concentration.
† Average percent leaf area on flag leaves of four randomly selected plants per cultivar per treatment in one replication after 46 days of treatment.
Plant height and number of heads/m were determined at harvest.

0.020 ppm (3-hr peak mean), and 0.033 ppm (1-hr peak mean). The elevated SO_2 concentrations occurred mostly outside of the 0900–1600 CST O_3 addition period—60% of the 1-hr peak mean values occurred between 2100 and 0300. On 6 days the 3-hr peak values occurred at least partly during the 7-hr O_3 addition period.

Foliar injury

Detailed injury evaluations were not made in 1982, but subjective observations found chlorotic leaves on some plants of all cultivars in all O_3 addition treatments above ambient (NF) after 11 days of exposure. Flowering began after 20 days of exposure, and most plants in all treatments (except CF) exhibited some chlorosis. Necrotic tissue was noted on many plants in the NF+0.06 and NF+0.09 ppm treatments at that time. In 1983, foliar injury symptoms developed more slowly than in 1982; but, there was considerable injury noted on both cultivars in all O_3 treatments above ambient (NF) after 46 days of exposure

Table 3. Plant height and number of heads/m of row for three cultivars of winter wheat exposed to selected O_3 treatments in open-top field chambers for 55 days in 1982

		Abe		Arthur-71		Roland	
Treatment	O_3* (ppm)	Height (cm)	Number of heads/m	Height (cm)	Number of heads/m	Height (cm)	Number of heads/m
AA	0.042	75	104	77	101	78	103
CF	0.023	76	91	79	78	80	82
NF	0.041	78	101	81	87	81	75
NF+0.03	0.068	75	89	77	78	78	84
NF+0.06	0.095	74	87	77	87	76	86
NF+0.09	0.122	72	114	75	84	75	72

* Seasonal 7-hr/day mean concentration.

(Table 2). While both cultivars exhibited a similar total amount of injury in all treatments, 'Arthur-71' exhibited considerably more necrotic tissue than 'Abe' at the two highest O_3 treatments (NF + 0.04 and NF + 0.06 ppm).

Growth and yield

While there was a trend toward reduced plant height in the highest O_3 treatment in both years, the differences were not significant ($P = 0.05$) (Tables 2 and 3). The plants in 1983 were 10–15 cm taller than normal (according to Extension Service estimates) and 30–40% taller than they had been in 1982. This was probably due to the excessive rainfall (18.6 cm) in May of 1983, and this increased height resulted in lodging of plants in some plots (severe in three plots) prior to anthesis. Also, heading began 8 days later in 1983 (27 vs 19 May in 1982) and flowering began 12 days later (9 June vs 28 May in 1982). Initiation of spring growth appeared to begin about the same time in both years, as did final crop senescence. There appeared to be treatment differences in the number of heads/m (significant only for 'Abe' in both years) but these were not related to the O_3 concentration because the numbers of heads/m had already been determined when the exposures began (Tables 2 and 3).

Split-plot analysis of covariance of the 1982 data for overall grain yield (using O_3 treatments as the main plot, cultivar as the subplots, and number of heads/m as the covariate) indicated highly significant ($P = 0.001$) effects due to O_3, cultivar, $O_3 \times$ block, $O_3 \times$ cultivar, and number of heads/m. A similar analysis of the 1983 data indicated significant ($P = 0.05$) effects due to O_3, cultivar, and number of heads/m.

The analysis of variance (or covariance) of the 1982 data for each cultivar indicated highly significant ($P = 0.001$) O_3 effects on grain yield and 100-seed wt (Table 4). The O_3 effects on number of seeds/m were also significant ($P = 0.05$ for 'Abe' and 'Arthur-71,' and $P = 0.001$ for 'Roland'). The effects on number seeds/head were significant for 'Roland' ($P = 0.001$) and 'Arthur-71' ($P = 0.05$), but not for 'Abe'. None of the block effects was significant, but the covariate (number of heads/m) was always highly significant ($P = 0.001$).

The results of the analyses of variance (or covariance) of the 1983 data indicated significant O_3 effects on grain yield and 100-seed wt ($P = 0.05$) for 'Arthur-71', and 100-seed wt ($P = 0.01$) and number of seeds/head ($P = 0.05$) for 'Abe' (Table 4). There were some significant block effects indicating that the blocking design was effective in explaining a significant amount of the total variation (i.e. removing that variation from the estimate of experimental error). The covariate (number of heads/m) was significant ($P = 0.05$) for number of seeds/m and stem weight/m for both cultivars.

As the concentration of O_3 increased, there was a general decrease in the yield variables (grain yield, 100-seed wt, number of seeds/m, and number of seeds/head) for all three cultivars in 1982 (Table 5). The yield reductions for 'Abe' and 'Arthur-71' were very similar for all yield variables, with the overall grain yield reductions due primarily to reduced seed number in the NF treatment but due mainly to reduced individual seed weight (100-seed wt) in the three O_3 addition treatments. The overall grain yield reduction for 'Roland' was similar to the other two cultivars at the NF treatment, but due entirely to reduced individual seed weight. In the higher O_3 treatments, the grain yield was reduced considerably more for 'Roland', but (as with the other two cultivars) reductions in seed numbers accounted for about one-third of the overall grain yield reduction.

The yield data for 1983 indicated little or no effect of the lower O_3 treatments (NF and NF + 0.02), but then general reductions in the weight variables as O_3 increased (Table 6). The overall grain yield reductions for both cultivars were apparently caused entirely by reductions in individual seed weight. The number of seeds per head was slightly increased in all of the O_3 addition treatments, which tended to mediate the effects of reduced individual seed size on overall grain yield. Stem weights were also reduced as O_3 increased above ambient, but not as much as the grain weights were.

The results of the t-test comparing the NF and AA treatments to evaluate the chamber effect indicated no differences for any of the variables in 1982 except number of heads/m of 'Roland', and only for 100-seed wt of 'Arthur-71' in 1983. There

Table 4. *Results of the analysis of variance (and covariance) tests using only the chambered plot data to determine significance of block and* O_3 *treatment effects on the yield of three winter wheat cultivars exposed to* O_3 *in open-top field chambers for* 55 *days in* 1982 *or* 53 *days in* 1983

		Mean squares											
		Abe				Arthur-71				Roland			
Source (1982)	d.f.	Kg/ha†	100-seed wt	No. seeds/m	No. seeds/ head	Kg/ha	100-seed wt	No. seeds/m	No. seeds/ head	Kg/ha	100-seed wt	No. seeds/m	No. seeds/ head
Blocks	3	169,055	0.007	25,595	0.88	144,995	0.0297	15,710	2.92	139,137	0.074	7151	0.62
Ozone	4	4,990,533***	2.335***	83,477*	4.27	3,203,321***	2.066***	41,907*	7.11*	6,946,512***	2.408***	248,235***	44.66***
No. heads	1	8,484,732***	—	1,760,288***	—	7,208,249***	—	1,540,271***	—	5.066,235***	—	1,629,274***	—
Residual	12(11)‡	(201,218)	0.044	(15,076)	2.54	(61,234)	0.049	(7775)	1.36	(183,070)	0.051	(15,140)	1.60
CV		10.7	5.8	6.0	7.5	6.7	6.0	5.0	5.5	12.1	8.3	5.4	4.5

		Abe					Arthur-71				
Source (1983)	d.f.	Kg/ha	100-seed wt	No. seeds/m	No. seeds/ head	Stem wt/m (g)	Kg/ha	100-seed wt	No. seeds/m	No. seeds/ head	Stem wt/m (g)
Blocks	2	2041	0.078*	13,621	6.55***	6826*	295,196	0.017	39,668*	3.51	5297
Ozone	4	328,999	0.108**	8949	1.34*	465	448,600*	0.126*	30,940	1.83	1352
No. heads	1	646,730	—	185,881*	—	5502*	75,726	—	188,714**	—	9548*
Residual	5(4)§	(86,918)	0.009	(11,309)	0.14	(408)	(54,226)	0.022	(5517)	2.11	(938)
CV		5.0	2.9	3.3	1.9	4.3	4.6	5.1	2.4	6.7	7.1

† Kg/ha, No. seeds/m, and stem weight were tested by analysis of covariance using No. heads/m as the covariate.
‡ Numbers in parentheses are from analysis of covariance.
§ Residual d.f. are low because data from three plots in one block were discarded due to severe early lodging. All mean squares were determined from Type III sums of squares.
*, **, *** Significant at $P = 0.05$, 0.01, and 0.001, respectively.

Table 5. Yield responses of three cultivars of winter wheat exposed to charcoal-filtered air (CF), ambient air open plot (AA), and ambient air plus O_3 in open-top chambers for 7-hr/day for 55 days during 1982

Treatment	O_3* (ppm)	Abe: No. seeds/m†	Abe: No. seeds/head	Abe: Kg/ha†	Abe: 100-seed wt (g)	Arthur-71: No. seeds/m	Arthur-71: No. seeds/head	Arthur-71: Kg/ha	Arthur-71: 100-seed wt (g)	Roland: No. seeds/m	Roland: No. seeds/head	Roland: Kg/ha	Roland: 100-seed wt (g)
AA	0.042	2430	25.1	5811	4.25	1965	22.5	4746	4.23	2834	32.4	5771	3.56
CF	0.023	2226	22.5	5315	4.29	1892	23.1	4647	4.32	2469	30.8	5007	3.64
NF	0.041	2035	21.4	5050	4.36	1802	21.6	4300	4.26	2472	30.9	4668	3.32
NF+0.03	0.068	2192	22.1	4633	3.80	1801	21.8	3958	3.94	2323	29.1	3557	2.73
NF+0.06	0.095	2091	20.6	3606	3.10	1706	20.6	3151	3.24	2124	26.8	2455	2.07
NF+0.09	0.122	1743	20.0	2736	2.60	1621	19.6	2412	2.65	1881	22.9	1859	1.83
		% of CF treatment				% of CF treatment				% of CF treatment			
AA		109	112	109	99	104	97	102	98	115	105	115	98
NF		91	95	95	102	95	94	93	99	100	100	93	91
NF+0.03		98	98	87	89	95	94	85	91	94	94	71	75
NF+0.06		94	92	68	72	90	89	68	75	86	87	49	57
NF+0.09		78	89	51	61	86	85	42	61	76	74	37	50

* Seasonal 7-hr/day mean concentration.
† Number of seeds/m and kg/ha are adjusted values from covariance analysis using number of heads (by cultivar) as the covariate.

Table 6. Yield responses of two cultivars of winter wheat exposed to charcoal-filtered air (CF), ambient air open plot (AA), and ambient air plus O_3 in open-top chambers for 7-hr/day for 53 days during 1983

		Abc					Arthur-71				
Treatment	O_3* (ppm)	No. seeds/m†	No. seeds/head	Kg/ha†	100-seed wt (g)	Stem wt/m (g)†	No. seeds/m	No. seeds/head	Kg/ha	100-seed wt (g)	Stem wt/m (g)
AA	0.045	3037	21.0	6381	3.68	130	3429	22.3	6695	3.47	130
CF	0.018	3080	18.9	5808	3.44	124	2995	20.2	5151	3.10	115
NF	0.044	3295	18.6	5986	3.45	126	3271	22.6	5622	3.13	124
NF+0.02	0.062	3163	20.3	5982	3.36	117	3125	21.7	5214	3.04	113
NF+0.04	0.078	3175	19.8	5762	3.26	119	3252	21.4	4943	2.73	107
NF+0.06	0.095	3042	19.5	4939	2.88	112	3098	21.9	4397	2.59	109
		% of CF treatment					% of CF treatment				
AA		99	111	110	107	105	114	110	130	112	113
NF		107	98	103	100	102	109	112	109	101	108
NF+0.02		103	107	103	98	94	104	107	101	98	98
NF+0.04		103	105	99	95	96	109	106	96	88	93
NF+0.06		99	103	85	84	90	103	108	85	84	95

* Seasonal 7-hr/day mean concentration.

† Number of seeds/m, kg/ha, and stem wt/m are adjusted values from covariance analysis using number of heads (by cultivar) as the covariate.

Table 7. Weibull model partitioning of variance in ozone × cultivar 2-way table for three cultivars of winter wheat exposed to O_3 in open-top chambers for 55 days in 1982

Source†	d.f.	SS	MS	F‡	R^2§
Total (O+C)	30	87,969,538			
Simple model	6	76,950,945			0.84
Common model	8	82,174,783			0.90
Full model	12	85,626,515			0.94
Lof	18	2,343,023	130,168	1.08	
Common–Simple	2	5,223,838	2,611,919	21.73***	
Full–Common	4	3,451,732	862,933	7.18**	

† Total (O+C) SS = the sum of the O_3, block, cultivar, O_3 × block, O_3 × cultivar, and number of heads (covariate) sums of squares from the split-plot analysis of covariance.

Simple model = SS (Weibull model with 1α, 1σ, 1c, 3 blocks, 1 covariate)—the correction factor; requires same yield level and response to O_3 for all three cultivars.

Common model = SS (Weibull model with 3α, 1σ, 1c, 3 blocks, 1 covariate)—the correction factor; allows different yield level for each cultivar but requires same proportional response to O_3.

Full model = SS (Weibull model with 3α, 3σ, 3c, 3 blocks, 1 covariate)—the correction factor; allows each cultivar to have its own yield level and response to O_3.

Lof = Total (O+C) SS—Full model SS; measures lack of fit.

Common-Simple; tests cultivar differences in absolute yield.

Full-Common; tests cultivar differences in proportional response to O_3.

‡ Residual MS from split-plot analysis of covariance (120, 181 with 29 d.f.) was used for testing; this is not strictly valid because of method differences in handling block and covariate effects, but the Weibull residual was very close to the analysis of variance residual.

§ R^2 = amount of total sum of squares (91,454,796) explained by the model.

, * Significant at $P = 0.01$ and 0.001, respectively.

was a trend for fewer seeds/head in 1982 and for both fewer seeds/head and lower 100-seed wt in 1983 in the chambers.

Exposure–response models

Weibull regression models were fit to the data and the statistics for the models of the 1982 data are presented in Table 7. The common model, where each cultivar has a different α but a common σ and c, was a significant improvement over the simple model ($F = 21.73$) indicating a significant cultivar difference in yield at 0.00 ppm O_3. The full model, where α, σ, and c differ for each cultivar, was a significant improvement over the common model ($F = 7.18$), indicating a significant cultivar difference in response to O_3 as well. A further breakdown of the 1982 data indicated that 'Abe' and 'Arthur-71' were homogeneous in response to O_3, and 'Roland' was responsible for the heterogeneous response noted in Table 7. The regressions from the full Weibull model are displayed in Fig. 3. The greater sensitivity of 'Roland' to O_3 is evidenced by the steeper slope. The model parameters are given in Table 8.

Regression analyses of the 1983 data showed no differences between the two cultivars in terms of absolute yield or proportional response to O_3. Combined ('Abe' and 'Arthur-71') models were also generated to test the O_3 responses across the two years (Table 9). The residual mean square from the fullest model was used to test the models in the combined analysis over the two years. The models indicated a significant ($P = 0.05$) year effect but no cultivar heterogeneity or O_3 × year interaction. The year effect was just significant ($P = 0.05$), but there was not much O_3 response in 1983 so the precision on the parameter estimates (Table 8) was not very good (standard errors are large). Thus a common response model for both cultivars over both years was also produced ($R^2 = 0.87$).

Relative grain yield performance curves for the three cultivars are plotted in Fig. 4.

There appeared to be less of an O_3 effect on

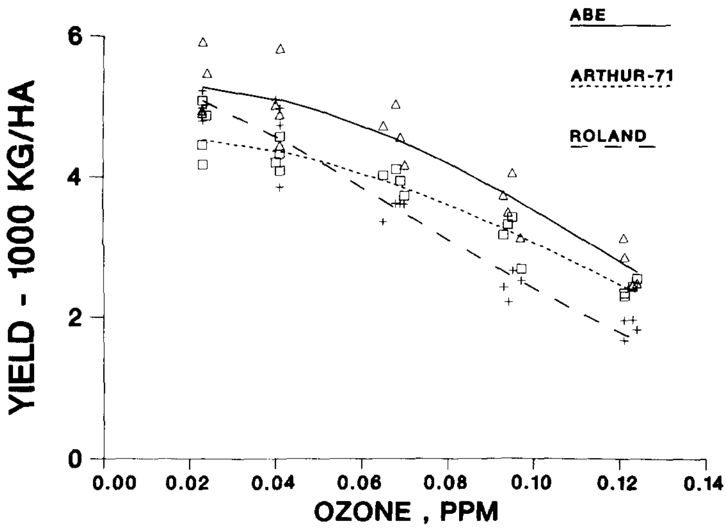

FIG. 3. Weibull model regression curves and individual plot points for three winter wheat cultivars indicating grain yield as a function of the 1982 7-hr/day seasonal mean O_3 concentration.

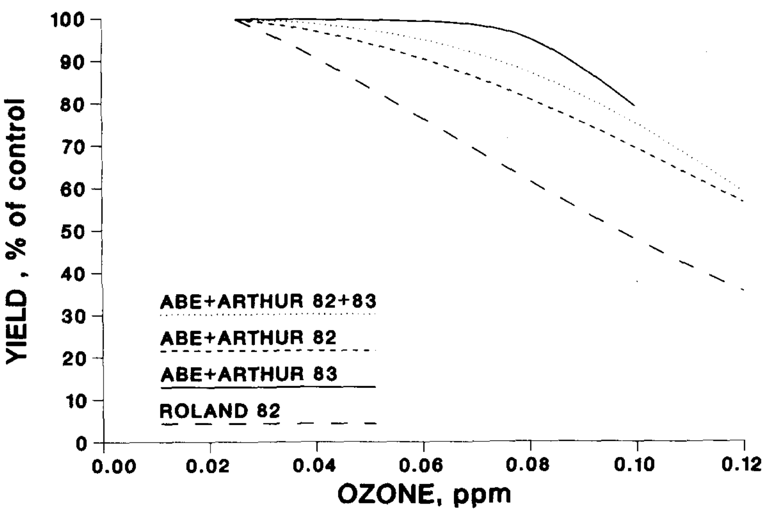

FIG. 4. Relative winter wheat grain yield (kg/ha) performance curves from fitted Weibull models for three cultivars indicating grain yield as a function of 7-hr/day seasonal mean O_3 concentration, using a reference concentration of 0.025 ppm. The responses of 'Abe' and 'Arthur-71' were not significantly different ($P = 0.05$) from each other in either 1982 or 1983, but the combined responses were different between 1982 and 1983.

Table 8. Parameters for the fitted Weibull equations for overall grain yield of three winter wheat cultivars exposed to O_3 (7-hr/day, 7 days/week) for 55 days in 1982 and of two winter wheat cultivars exposed to O_3 for 53 days in 1983 at Argonne, IL

Parameter*	Abe 1982	Arthur-71 1982	Roland 1982	Abe 1983	Arthur-71 1983	Abe and Arthur-71 1982	Abe and Arthur-71 1983	Abe and Arthur-71 1982 and 1983
α	5235 (345)†	4513 (293)	5426 (325)	5873 (222)	4910 (307)	4877 (275)‡	5641 (223)‡	5295 (226)§
σ	0.153 (0.15)	0.146 (0.014)	0.113 (0.005)	0.108 (0.024)	0.148 (0.071)	0.150 (0.010)	0.123 (0.028)	0.145 (0.008)
c	2.272 (0.823)	2.580 (0.935)	1.734 (0.330)	14.400 (26.225)	3.781 (3.902)	2.378 (0.612)	7.060 (6.137)	3.326 (0.655)

* α = grain yield at 0.00 ppm of O_3; σ = concentration in ppm at which yield is 0.37; c = dimensionless shape parameter.
† Values in parentheses are 1 S.E.
‡ Mean of the two α-values for each cultivar generated by the 'Common 2' Weibull model.
§ Mean of the four α-values for both cultivars generated by the 'Common 1' Weibull model.

yield at the lower O_3 concentrations (0.04–0.06 ppm) in 1983, although the model parameter estimates were rather poor (note S.E. estimates for c in Table 8). The cultivar 'Roland' was significantly more sensitive to O_3 in 1982 than 'Abe' and 'Arthur-71' were in either year, especially at the lower concentrations (0.04–0.06 ppm).

A comparison of the responses of winter wheat to O_3 with the responses of other crops studied in the NCLAN program at Argonne National Laboratory showed that 'Abe' and 'Arthur-71' were more sensitive than grain sorghum or field corn and less sensitive than soybean (Fig. 5). 'Roland' was the most sensitive crop cultivar studied thus far.

DISCUSSION

The results of this study indicate potential yield losses in winter wheat in many of the crop growing areas. Depending upon cultivar, yield reductions could approach 23% at an O_3 concentration of 0.06 ppm (7-hr/day seasonal mean) compared to a control of 0.025 ppm. A previous study with four other soft red winter wheat cultivars indicated up to 11% yield loss at 0.06 ppm O_3.[4] There were significant cultivar differences noted in this study, and the most sensitive cultivar was predicted to have a 9% yield reduction at only 0.04 ppm O_3, a lower mean concentration than that recorded in most regions of this country.[12] The yield loss estimates at the higher O_3 concentrations ($>$ 0.10 ppm) were probably conservative in this study because the grain was hand harvested and threshed—many of the shrivelled dry seeds counted in this study would have been lost during machine harvesting.

The major effect of O_3 appeared to be on seed size rather than seed number. This is in agreement with previous wheat research in which acute (0.2 ppm, 4-hr/day, 7 days) O_3 exposures during anthesis did not significantly reduce the number of seeds produced per head, but did reduce kernel weight.[13] It is also in agreement with work on field corn[8] and grain sorghum,[10] where yield reductions up to about 25% were ascribed almost entirely to reductions in individual seed weight. Such was not the case with soybean, where reductions in pod number were about equally as important as seed weight in causing overall yield

Table 9. Weibull model partitioning of variance in O_3 × cultivar 2-way table for two cultivars ('Abe' and 'Arthur-71') of winter wheat exposed to O_3 in open-top chambers for 55 days in 1982 and 53 days in 1983

Source†	d.f.	SS	MS	F‡	R^2§
Common 1 model	11	88,705,031			0.87
Common 2 model	13	90,300,843			0.89
Full model	17	90,652,488			0.89
Lof	46	10,916,090	237,306	1.00	
Common 2–Common 1	2	1,595,812	797,906	3.36*	
Full–Common 2	4	351,645	87,911	0.37	

* Significant at $P = 0.05$.

† Common 1 model = SS (Weibull model with 4α, 1σ, $1c$, 3 blocks in 1982, 2 blocks in 1983, 1 covariate)—correction factor; allows different yield level for each cultivar and year but requires same proportional response over cultivars and years to O_3.

Common 2 model = SS (Weibull model with 4α, 2σ, $2c$, 3 blocks in 1982, 2 blocks in 1983, 1 covariate)—correction factor; allows different yield level for each cultivar and year, a different proportional response to O_3 in each year, but requires the same proportional response over cultivars within year.

Full model = SS (Weibull model with 4α, 4σ, $4c$, 3 blocks in 1982, 2 blocks in 1983, 1 covariate)—correction factor; allows each cultivar to have its own yield level and response to O_3 in each year.

Lof = Total (corrected) SS—Full model SS; measures lack of fit.

Common 2–Common 1; tests homogeniety of proportional response to O_3 over the 2 years.

Full–Common 2; tests homogeniety of proportional response to O_3 of the cultivars within each year.

‡ Residual MS from Full Weibell model (237,306 with 48 d.f.) was used for testing.

§ R^2 = proportion of total sums of squares (101,568,578) explained by the model.

reduction.[9] Decreases in seed size rather than seed number would indicate effects to photosynthate production or allocation, or accelerated senescence, rather than effects to flowering, pollination, or ovule survival.

Ozone sensitivity was less in 1983 than it had been in 1982. The moisture levels were much greater in 1983, especially in May. While this might suggest the crop should have been more sensitive to O_3 in 1983, the data of HEGGESTAD[7] suggest that moisture stress may potentiate, rather than moderate, O_3 effects at near ambient concentrations. The 1982 wheat may have been under some moderate moisture stress and thus more sensitive to moderate O_3 stress. Alternatively, although the seasonal mean O_3 concentrations were similar, the mean O_3 in May 1982 was about 10% higher than in June, while in 1983 the O_3 was about 30% lower in May than in June. This could have led to effects occurring earlier in the season in 1982 (prior to and during anthesis). This thought is verified by three facts. Foliar injury developed earlier and more rapidly in 1982, numbers of seeds per head were reduced in 1982 but not in 1983, and stem weight was not affected as much as was grain weight in 1983. Also, heading and flowering developed 8–12 days earlier in 1982 than in 1983, while initiation of spring growth and final senescence occurred at about the same time in both years. It seems reasonable to suggest that the higher May 1982 O_3 concentrations caused an earlier shift to the reproduction phase of plant development, and affected not only seed number but also seed size due to accelerated senescence of the vegetative tissues. It would seem that in future studies such as

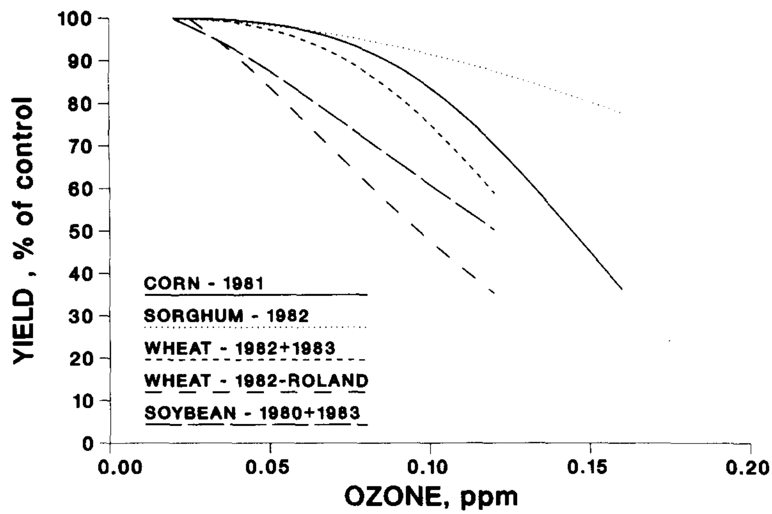

FIG. 5. Relative crop yield (kg/ha) performance curves from fitted Weibull models for grain sorghum, field corn, winter wheat, and soybean indicating seed yield as a function of 7-hr/day seasonal mean O_3 concentration, using a reference concentration of 0.025 ppm.

the one described herein, some attention should be given to describing, in some detail, the temporal variations in O_3 concentrations across the season correlated with a more critical evaluation of crop phenology (i.e. growth rates).

In the ongoing NCLAN economic modeling effort, the effects on crop yield obtained with response models serve as a starting point for the economic analysis. The economic modeling effort will be facilitated if various data sets on the same crops can be combined into one model. The analyses in this study have shown that the O_3 responses for two cultivars across 2 years may be different and one may question whether the cultivars can be combined into one response model. However, one cultivar does stand alone as having greater O_3 sensitivity. This cultivar variability needs to be examined further. Whether or not these data can be combined with the data of HEAGLE *et al.*[4] on four other wheat cultivars also needs to be (and currently is being) tested.

These results indicate that winter wheat may be more sensitive to O_3 than previously estimated,[4] and it appears considerably more sensitive than field corn or grain sorghum. While the O_3 sensitivity of wheat may be generally less than that of soybean, and wheat is grown in areas where O_3 concentrations may be lower, the presence of a very sensitive cultivar ('Roland') suggests potential yield reductions due to O_3. One must be cautious regarding extrapolation of these data beyond the conditions of the experiments. Clearly, more research needs to be done to better identify cultivar and year-to-year variability, and to elucidate how O_3 effects to plant growth are translated into yield reductions.

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