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Effects of Ozone on the Yield of Spring Wheat (*Triticum aestivum* L., cv. Albis) Grown in Open-Top Field Chambers

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ABSTRACT

*Spring wheat (*Triticum aestivum *L., cv. Albis) was grown in the field at a site located in central Switzerland, and exposed to chronic doses of ozone (O_3) in open-top chambers to study impacts on yield. The experiment was carried out in 1986, 1987 and 1988. The treatments used included charcoal-filtered air (CF), non-filtered air (NF) and non-filtered air to which constant amounts of O_3 (two levels, O_3-1 and O_3-2) were added daily from 09.00 until 17.00 local time. Mean solar radiation-weighted O_3 concentrations during the fumigation period were in the range 0·016–0·022 μl litre^{-1} (CF), 0·036–0·039 μl litre^{-1} (NF), 0·057–0·058 μl litre^{-1} (O_3-1, used in 1987 and 1988 only) and 0·078–0·090 μl litre^{-1} (O_3-2). Fumigation was maintained from the three-leaf stage until harvest. Ambient plots were used as a reference. Plant characteristics examined included straw yield, grain yield, number of grains per head, number of heads per surface area, weight of individual grains and harvest index (ratio of grain weight to total dry weight). Pollutant concentrations and other environmental parameters were monitored continuously inside and outside the chambers. In 1986 and 1987, enclosure mostly increased the values of different parameters, while in 1988, they were decreased. The negative enclosure effect was due to extremely turbulent winds, which caused lodging inside the chambers. In all 3 years, increasing O_3 concentrations negatively affected the*

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parameters studied, except for the number of heads per surface area, which showed no treatment response. Grain yield showed a very sensitive response to O_3. The effect of O_3 on grain yield was due to an effect primarily on grain size and secondarily on grain number. The relative response of grain yield to O_3 was similar in all 3 years, despite year-to-year differences in climatic conditions and enclosure effects. The analysis of the data for combined years revealed an increase of about 10% in grain yield due to air filtration. The corresponding increase in straw yield was only about 3·5%. Exposure–response models were developed for individual years and combined years. It is concluded that, in the study area, ambient O_3 may affect grain yield in spring wheat.

INTRODUCTION

Air pollution by ozone (O_3) can decrease the yield of agronomically important crops (Heck *et al.*, 1986). Based on studies with open-top chambers, yield losses due to O_3 of various crops have been estimated in different parts of the USA (Heck *et al.*, 1983). Comparatively little is known about the possible impacts of O_3 on crops in Europe (Roberts, 1984). In view of this lack of information, a co-ordinated experimental programme to evaluate crop losses due to air pollution in Europe was initiated by the Commission of the European Communities (CEC). The present study carried out in Switzerland was designed to accompany the CEC programme.

Based on air quality data, it was suggested that O_3 dominates the air pollution climate in an area including southern Germany, parts of Austria and Switzerland (Last *et al.*, 1986). From the analysis of present-day and historical O_3 data, it was suggested that average concentrations may have increased in Europe during the past century (Volz & Kley, 1988). Ozone concentrations observed during the growing season in central Switzerland often exceed 0·060 μl litre^{-1}, which is the National Air Quality Standard for the 1-h maximum O_3 concentration (Bundesamt für Umweltschutz, 1988). Episodes with peak concentrations above 0·06–0·07 μl litre^{-1} have been shown to cause visible damage to sensitive species (Becker *et al.*, 1989). Little is known, however, about the effect such O_3 exposure might have on the yield of agricultural crops. Based on observed reductions in wheat leaf photosynthesis, yield losses are expected to occur (Lehnherr *et al.*, 1988). The aim of this study was to evaluate possible effects of different levels of O_3 in ambient air on the yield of spring wheat, grown in a major agricultural area of the country, and to rank different components of yield according to their sensitivity to O_3.

Wheat is one of the major crops used in Swiss agriculture. In 1985, 32% of arable land was used for wheat production (Bundesamt für Statistik, 1986).

Only approximately 20% of the wheat cultivars used are spring sown. Nevertheless, a spring wheat cultivar was used for this study, in order to comply with the common protocol of the co-ordinated CEC programme, which prescribed the use of spring-sown crops. The effects of O_3 on wheat yield have previously been studied in the USA: Kress *et al.* (1985) observed higher O_3 sensitivity of wheat as compared to corn or sorghum. In the case of one cultivar (Roland), potential yield reductions due to ambient O_3 were suggested. Yield reductions due to ambient O_3 levels were also observed in experiments by Amundson *et al.* (1987) for the cultivar 'Vona', and for the cultivars 'Roland' and 'Vona' by Kohut *et al.* (1987). However, these results cannot be extrapolated to European conditions without caution. Significant cultivar and year-to-year variability, as observed by Heagle *et al.* (1979), Mulchi *et al.* (1986) and Kohut *et al.* (1987), indicate that different agronomic practices, and different soil and climatic conditions, can have an important effect on the response of crops to O_3.

In many earlier studies which evaluated O_3 effects on field-grown crops, open-top chambers were used (Heck *et al.*, 1983). Other techniques like open-air fumigation systems (McLeod *et al.*, 1988) have been used successfully for other pollutants. One of the advantages of using open-top chambers is that O_3 levels can be reduced below ambient concentrations. The CEC protocol suggests the use of open-top chambers for the co-ordinated project in Europe. This technique introduces a number of changes in the environmental conditions the plants are exposed to. These include changes in temperature, humidity, rainfall, radiation and wind velocity. The extent of the changes depends on the technical specifications of the fumigation system, as well as on-site conditions. It is thus important to investigate these changes and to relate them to differences in growth, development and yield between plants grown inside and outside of open-top chambers. In this paper, the effects from enclosure on different yield parameters are included, as well as the yield response to O_3.

MATERIALS AND METHODS

The 3-year experiment (1986–88) was conducted at Oeschberg (N47° 07′/E7° 37′). The site is located on the Swiss Central Plateau about 25 km north-east of Bern, at an altitude of 585 m above sea level. The nearest source of pollution is the highway N1 (Bern–Zurich) at a distance of about 2 km north-west from the site. The soil is a low humus loam with a pH of about 6·5. During the first and third year, the same field was used. During the second year, an adjacent field was used to enable crop rotation.

Spring wheat (*Triticum aestivum* L., cv. Albis) was used in all three years.

Prior to planting, NPK fertilizer was applied. Seeds ($200\,kg\,ha^{-1}$) were mechanically sown with 16·7 cm row-spacing. Open-top chambers were installed after the plants had emerged. Further cultural practices were the same inside and outside the chambers (e.g. fungicide application). Details of the timetable of events during the different experimental periods are summarized in Table 1.

Cylindrical open-top chambers, 1·5 m in diameter by 1·8 m in height, were constructed, as described by Fowler *et al.* (1988). Walls were made of corrugated Filon–Acrylresin sheets ('Suncall'), and were attached to aluminum rings at the top and at the bottom. One sheet was used as a door.

TABLE 1
Timetable of Events during the Experiments of 1986, 1987 and 1988

Event	*1986*	*1987*	*1988*
Planting and NPK-fertilization	09/04[a] (46)[b]	03/04 (60)	05/04 (80)
Plant emergence	28/04	18/04	14/04
Herbicide application	04/05	23/04	
N-Fertilization	06/05 (29)		02/05 (32)
Installation of open-top chambers	06/05	27/04	04/05
Begin daily O_3-fumigation	21/05	13/05	13/05
N-Fertilization		26/06 (30)	
Begin anthesis inside chambers	23/06	29/06	15/06
Begin anthesis in open field	29/06	05/07	19/06
Fungicide applied	04/07	02/07	
Harvest inside chambers	31/07	10/08	01/08
Harvest of ambient plots	08/08	13/08	01/08

[a] Day/month.
[b] Values in parentheses: kg N ha^{-1}.

A frustum of transparent PVC with an angle of 30° was placed on top of the cylinder leaving an open surface area of 1·06 m^2. Air was forced by a pump (Fischbach CFE 840/E-350-E) through a flexible pipe entering the chamber close to the base. This pipe supplied a perforated polyurethane annulus (10 cm diameter) attached to the inside of the chamber wall. The annulus was placed about 10 cm above the canopy and was moved up parallel to the growing crop. Each pump was adjusted manually to obtain three exchanges of the chamber volume per minute. During the first year, ventilation of the chambers was maintained all day and night at equal rates. During the second and third years, pumps were turned off between 22.00 and 07.00 h, in order to allow dew formation on the vegetation inside the chambers during the night.

In 1986, three treatments in open-top chambers were used: charcoal-filtered air (Camcarb 2000) (CF), non-filtered air (NF) and non-filtered air to which approximately 0·06 μl litre^{-1} O_3 was added daily from 09.00 until 17.00 h (O_3-2). In 1987, an additional treatment was introduced: non-filtered air with 0·03 μl litre^{-1} O_3 added (O_3-1). All four treatments were used again in 1988. Four ambient field plots without chambers were used for comparison (AA).

Ozone was generated by electrical discharge (Fischer 500M ozone generator) in pure oxygen (to avoid the formation of oxides of nitrogen) supplied from a tank. Ozone addition to non-filtered air was controlled by a clock and was maintained between 09.00 and 17.00 h local time. The amount of ozone added was kept constant. When necessary, the generator was adjusted manually.

Ozone exposure was characterized by the radiation-weighted average concentration during the fumigation period according to Rawlings *et al.* (1988):

$$[O_3]_i = \sum(w_i x_i)/\sum w_i$$

where w_i is solar radiation (W m^{-1}) and x_i is O_3 concentration (μl litre^{-1}). This parameter characterizing dose was chosen because it takes into account the fact that, under many environmental conditions, O_3 uptake by plants is largely controlled by the opening of the stomata, which is strongly influenced by light intensity. The calculated dose parameter thus accounts for important diurnal differences in O_3 fluxes (Hicks *et al.*, 1987). It could be calculated from measurements that were routinely carried out during these experiments.

Environmental variables were monitored in one open-top chamber of each treatment and in an open-field plot. Measurements inside chambers were performed on a 15-min per plot time-share system. Values were stored as 15-min averages. Continuous measurements were carried out in the open field and values were stored as 30-min averages. Routinely, measurements in other chambers of each treatment were carried out to check for chamber-to-chamber differences. Gas sampling lines (PTFE Teflon, 10 mm diameter) were insulated and heated to about 10°C above ambient temperature to avoid condensation of water. Air was sampled about 10 cm above the canopy. Sampling line efficiencies in transmitting O_3 were checked before and after the experiments. Losses of 3–10% were noted and concentrations measured were corrected accordingly. Ozone was measured with two monitors (Dasibi 1003 AH). One served for the measurements in the different chamber treatments, the other for the measurements in ambient air. Nitrogen oxides (NO, NO_2) were measured with one monitor (Tecan CLD 502) in the CF, O_3-1, O_3-2 and AA treatments, only. During the experiment, NO and NO_2 concentrations in the NF treatment were periodically compared with concentrations in the open field. At no time was a difference of more than 0·005 μl litre^{-1} NO_2 noted.

Air temperature, humidity and solar radiation were measured 10 cm above the canopy, soil temperature at 5 cm below ground. Precipitation was sampled with funnels in the centre of one chamber and in the open field. During the third year, four additional funnels were installed in one chamber. They were placed 20 cm from the chamber wall in N, S, W and E directions. This arrangement was used to determine the spatial variation in precipitation inside and outside the chambers. At different places in the open field, soil water content was recorded gravimetrically twice a week. Soil cores were taken at 0–30, 30–60 and 60–90 cm.

At the end of the experiment, four 50-cm row sections were harvested by hand in each chamber and open field plot. Samples were not taken closer than 10 cm to the chamber wall. After counting the number of heads, the grain was hand-threshed, cleaned, oven-dried to < 1% moisture content and then weighed. The number of grains per sample was counted and used to calculate the weight of individual grains from the total grain weight. Straw weight was determined after drying at 80°C for 24 h. The harvest index was calculated as the ratio between grain weight and total dry weight.

A total of 12 chambers was used in 1986, and 16 chambers in 1987 and 1988. Four measurements in each chamber were used to calculate the chamber mean of each variable. Two neighbouring chambers of the same treatment, which were connected to the same blower, formed a statistical unit. Four units, with one unit of each treatment, formed a replication. Each experiment thus consisted of two true replications. For the statistical analysis, the data from the 3 years needed to be combined, in order to obtain a sufficient number of true replications. Hierarchical analysis of variance was performed on the combined data and significant differences between treatment means (only chamber treatments) were identified with Duncan's multiple range test using the statistical package MSTAT developed by Michigan State University.

RESULTS

Climatic parameters

The three experimental periods differed in weather conditions; 1986 was characterized by rainy weather until the middle of June, which was followed by dry and sunny weather during the second half of the experiment. In 1987, dry weather occurred at the beginning of the experiment (May) and during the first half of July. Between and after these periods, intensive rainfalls were recorded frequently. Often soils were flooded, with water contents exceeding field capacity. In 1988 it was wet in May and early June. Later, mostly warm and sunny weather prevailed, but heavy thunderstorms and on one occasion complete flooding of the experimental field occurred. Especially inside the chambers, plants suffered from strong wind. Precipitation and O_3 data for ambient conditions are summarized for individual months and years in Table 2. During all three experiments, the time of anthesis was characterized by warm and sunny weather.

TABLE 2
Precipitation and O_3 Concentrations under Ambient Conditions for Individual Months during the Experimental Periods of 1986, 1987 and 1988

Month	*Precipitation*			O_3		
	1986 (mm)	*1987 (mm)*	*1988 (mm)*	*1986 (μl litre^{-1})[a]*	*1987 (μl litre^{-1})[a]*	*1988 (μl litre^{-1})[a]*
April	172	74	43		0·021/0·076	0·027/0·067
May	165	138	109		0·021/0·061	0·026/0·067
June	138	214	225	0·028/0·079	0·024/0·057	0·026/0·081
July	66	116	59	0·028/0·079	0·027/0·082	0·023/0·091
(Total	541	542	432)			

[a] 24-h average/1-h maximum concentration.

The effect of the chamber construction on the microclimatic conditions was assessed by comparing various parameters measured inside and outside of the chambers. Table 3 summarizes some of the differences observed in the different years for temperature, humidity, soil temperature and global radiation. The data show that the differences observed during the 3 years were similar. The increase in air temperature of +2·1°C due to the chamber was partly due to the fact that some heat from the motor inside the pump unit was transferred to the air entering the chambers (on an average about 1°C). Largest differences in air and soil temperature occurred between chambers of the O_3-2 treatment and ambient conditions. Importantly, it was noted that, for all parameters monitored, a spatial gradient inside the chambers existed, which is not accounted for by the data from point measurements given in Table 3. Precipitation measured in the centre of the chambers was reduced by 18, 3 and 12% in 1986, 1987 and 1988, respectively. There was a much stronger reduction in precipitation at other points in the chambers (data not shown). Overall reduction in 1988 was 30%. This reduction in precipitation was probably the largest of all modifications introduced by the chamber construction.

TABLE 3
Mean Values for Climatic Parameters Recorded in the Open Field (AA) and inside Open-Top Chambers (CF and O_3-2 Treatments) during the Experimental Periods of 1986, 1987 and 1988 and for Combined Years

Parameter	*Year*	*AA*	*CF*	*O_3-2*
Air temperature (°C)	1986	19·6	21·8 (+2·2)[a]	22·0 (+2·4)
	1987	17·7	19·8 (+2·1)	20·1 (+2·4)
	1988	16·2	18·1 (+1·9)	18·9 (+2·7)
	Average	17·8	19·9 (+2·1)	20·3 (+2·5)
Soil temperature (°C)	1986	19·4	20·1 (+0·7)	21·6 (+2·2)
	1987	19·2	19·7 (+0·5)	21·8 (+2·6)
	1988	17·0	17·4 (+0·4)	19·7 (+2·7)
	Average	18·5	19·1 (+0·5)	21·0 (+2·5)
Relative humidity (%)	1986	82·0	74·5 (−7·5)	77·5 (−4·5)
	1987	86·0	85·4 (−0·6)	81·7 (−4·3)
	1988	83·7	81·2 (−2·5)	79·1 (−4·6)
	Average	83·9	80·4 (−3·5)	79·4 (−4·5)
Solar radiation (Wm^{-2})[b]	1986	447	375 (−72)	380 (−66)
	1987	431	400 (−31)	397 (−34)
	1988	553	410 (−143)	417 (−136)
	Average	477	395 (−82)	398 (−79)

[a] Values in parentheses indicate the differences from the AA treatment.
[b] Values for the period between 09.00 and 17.00 h local time.

Pollutant exposure

Measurements of NO and NO_2 concentrations in the different chamber treatments revealed very small differences between them. Concentrations of NO were generally below 0·005 μl litre^{-1}. Average NO_2 concentrations in ambient air during the fumigation periods were 0·019, 0·014 and 0·015 μl litre^{-1} in 1986, 1987 and 1988, respectively. Filtration with activated charcoal (not impregnated to absorb NO_2) resulted in a reduction of approximately 0·005 μl litre^{-1}, and addition of O_3 to ambient air also caused no significant change in NO or NO_2 levels. No measurements of SO_2 were made. Generally, mean concentrations in rural areas of Switzerland during summertime are similar to NO concentrations (Bundesamt für Umweltschutz, 1988).

Figure 1 shows the average diurnal profile of solar radiation-weighted O_3 concentrations in the different treatments in 1988. Concentration profiles in 1986 and 1987 were very similar, but in 1986, no O_3-1 treatment was used. Due to the fact that constant amounts of O_3 were added in the O_3-1 and O_3-2 treatments, the change in radiation-weighted concentration at the

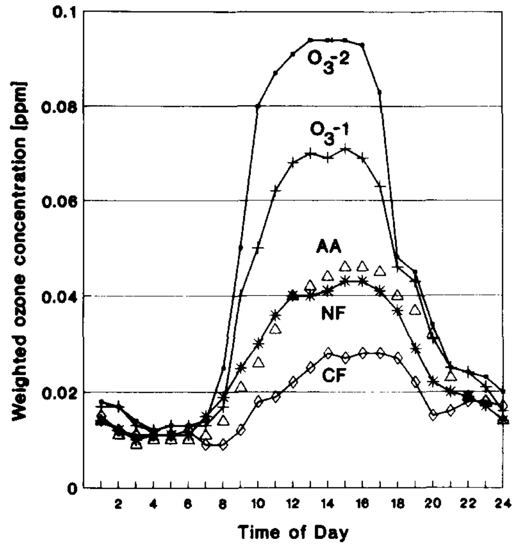

Fig. 1. Diurnal pattern of solar radiation-weighted concentrations of O_3 for each treatment during the exposure period in the 1988 spring wheat study at Oeschberg, Switzerland. AA = ambient air; NF = non-filtered air; CF = charcoal-filtered air; O_3-1 and O_3-2 = non-filtered air with O_3 added daily from 09.00 until 17.00 h local time.

beginning and at the end of the fumigation period was rapid, but less rapid than changes in unweighted concentrations.

Table 4 summarizes characteristics of O_3 exposure in the different chamber treatments: 24-h means averaged over the different experimental periods for the different treatments were similar in the 3 years. Larger differences between years occurred with respect to peak concentrations, but solar radiation-weighted means also did not differ much between years. Overall, with respect to O_3 exposure, the three experiments were comparable.

Visual foliar injury

Evaluations of visual injury symptoms were not made in detail. Subjective observations noted chlorotic leaves in the O_3-2 treatment only a few days after the beginning of the fumigation. In the O_3-1 treatment, chlorotic leaves appeared about 4 weeks after the beginning of the fumigation. The appearance of injury symptoms was somewhat confounded by the presence of powdery mildew (*Erysiphe graminis*). Strong infection occurred in 1986 and 1988. The degree of infection was consistently higher inside the chambers than in the open field. Again based on subjective evaluations, infection decreased with increasing O_3 concentration.

TABLE 4
Ozone Exposure Characteristics of each Treatment for Separate and Combined Years

Treatment	*Year*	*24-mean*	*Maximum*[a] *concentration* (μl *litre*$^{-1}$)	*Weighted mean*[b]
CF	1986	0·012	0·061	0·020
	1987	0·012	0·054	0·016
	1988	0·017	0·065	0·022
	Average	0·014	0·060	0·019
NF	1986	0·027	0·068	0·039
	1987	0·024	0·078	0·036
	1988	0·024	0·073	0·036
	Average	0·025	0·073	0·037
O_3-1	1986	—	—	—
	1987	0·036	0·122	0·057
	1988	0·036	0·110	0·058
	Average	0·036	0·116	0·058
O_3-2	1986	0·047	0·181	0·090
	1987	0·045	0·175	0·083
	1988	0·045	0·148	0·078
	Average	0·046	0·168	0·084
AA	1986	0·027	0·080	0·042
	1987	0·024	0·082	0·038
	1988	0·025	0·091	0·039
	Average	0·025	0·084	0·040

[a] For averaging times see Materials and Methods.
[b] Solar radiation-weighted mean ozone concentration.

Yield assessments

Differences in microclimatic conditions between chamber-enclosed and ambient plots resulted in differences in plant characteristics (Fig. 2). These differences varied from year to year. In 1986, plants inside chambers produced slightly higher straw and grain yield. The difference in grain yield was associated with larger grain weights. This increase could have been caused by the higher temperatures in the chambers. In the wet year of 1987, the reduction in precipitation inside the chambers reduced soil water content and avoided flooding of the soil. This protective effect of the chamber resulted in relatively larger straw and grain yields. The increase in yield was associated with a relatively larger number of grains per head. In 1988, stormy conditions caused mechanical stress to the plants. This affected the plants inside the chambers more than those outside. Under turbulent

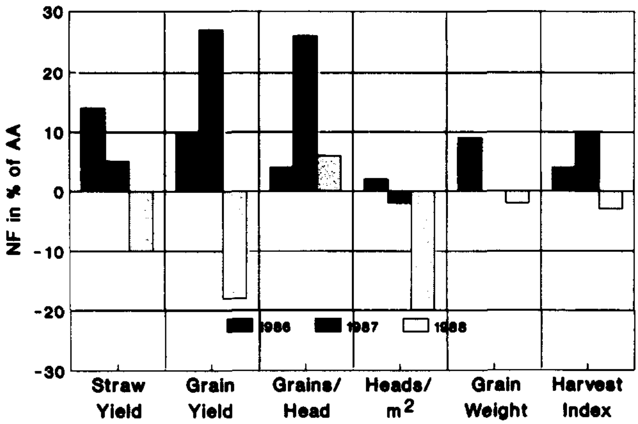

Fig. 2. The effect of enclosure on spring wheat yield in different years. Mean values obtained in four open-top chambers with non-filtered ambient air (NF) are compared to mean values obtained in open field plots (AA).

conditions, fast circular air movement was observed in the chambers, which caused lodging. Resulting reductions in straw and grain yield were associated with a reduced number of heads per surface area.

Table 5 contains mean values for straw yield, grain yield and grain yield components for each year and combined years. Absolute levels of straw and grain yield were highest in 1988. In the individual years, straw and grain yield decreased with increasing O_3 concentration. Although the differences between CF and NF treatments were small, they were consistent in the different years. Reductions in grain yield were associated with reductions in grain weight and—to a lesser extent—with reductions in the number of grains per head. The effect of O_3 thus appeared to be due to an effect primarily on the size of individual grains and secondarily on the number of grains. The number of heads per surface area was affected only at the highest O_3 level (O_3-2). The harvest index is a parameter which indicates the partitioning of dry matter between grain and straw, and is defined as the proportion of biological yield represented by economic yield. With increasing O_3 concentration, harvest indices tended to decrease, which indicated that relatively more dry matter was partitioned into straw as compared to grain. Based on the data for combined years, an overall increase in grain yield of 10% could be attributed to the effect of filtration, while straw yield increased by only 3%.

Hierarchical analysis of variance was performed on the data from combined years (Table 6). The effects of the O_3 treatment were highly significant ($P = 0{\cdot}001$) for straw and grain yields, grain weight and harvest index, and significant at $P = 0{\cdot}005$ for number of grains per head. Treatments had no significant effect on the number of heads per m^2. The

TABLE 5
Mean values of Straw Yield, Grain Yield and Grain Yield Components for Spring Wheat in the Different OTC-Treatments for Individual Years and for Combined Years

Treatment	*Straw yield ($t\ ha^{-1}$)*	*Grain yield ($t\ ha^{-1}$)*	*Grains per head*	*Heads per m^2*	*Grain weight (mg)*	*Harvest index (%)*
			1986			
CF	6·20	6·64	41·1	501·3	33·5	48·0
NF	6·17	6·11	39·0	522·0	30·7	45·9
O_3-2	4·73	2·56	29·1	491·3	20·3	33·8
			1987			
CF	6·74	6·17	34·6	530·0	33·7	43·7
NF	6·56	5·54	33·3	512·5	32·1	41·5
O_3-1	5·94	3·86	30·5	522·5	24·3	35·7
O_3-2	5·16	2·13	24·1	510·0	17·1	26·0
			1988			
CF	7·50	6·68	34·8	528·0	36·1	41·3
NF	7·02	6·11	36·0	475·5	35·7	42·8
O_3-1	6·07	4·61	32·1	509·0	27·6	38·7
O_3-2	4·06	2·31	25·3	431·0	21·2	31·7
			Combined years[a]			
CF	6·81 a	6·50 a	36·8 a	519·8 a	34·4 a	44·3 a
NF	6·58 ab	5·92 a	36·1 a	503·3 a	32·8 ab	43·4 a
O_3-1	5·99 ab	4·18 b	31·2 ab	516·7 a	25·7 bc	36·9 ab
O_3-2	4·71 b	2·33 c	26·2 b	481·6 a	19·4 c	30·4 b

[a] Means in one column followed by the same letter are not significantly different at $P = 0{\cdot}05$.

TABLE 6
Mean Squares from the Hierarchical Analysis of Variance for Straw Yield, Grain Yield, and Grain Yield Components for the Combined Years

Source	*df*	*Straw yield*	*Grain yield*	*Grains per head*	*Heads per m^2*	*Grain weight*	*Harvest index*
				Error mean square			
Ozone	3	10·1***	39·7***	273·7**	3 200·5	538·3***	470·6***
Year	7	1·0	0·4	33·2***	2 640·3	17·3***	39·4

***, **, *: Significant at $P = 0{\cdot}01$, $0{\cdot}05$ and $0{\cdot}1$.

direct comparison of means from combined years revealed no significant differences at $P = 0{\cdot}05$ for any of the parameters studied. Year-to-year differences in growing conditions increased the variation within each treatment. When each chamber was used as a single statistical unit, as done by Mulchi *et al.* (1986), the difference in grain yield between the CF and NF treatments was significant at $P = 0{\cdot}05$ in 1986, 1987 and for combined years (data not shown).

Grain yields determined in the different chamber treatments were related to the mean radiation-weighted O_3 concentration. These concentrations were calculated for the period during which the chambers were placed over the experimental plots. The length of this period was 86, 92 and 89 days in 1986, 1987 and 1988, respectively. Weibull functions were fitted to the data. These functions for spring wheat exposed to O_3 at Oeschberg (Switzerland) in the different years were as follows (yield in t ha^{-1} and O_3 exposure as radiation-weighted mean concentration in μl litre^{-1}):

$$
\begin{array}{ll}
\text{1986:} & \text{Yield} = 6{\cdot}70 \exp - (O_3/0{\cdot}090)^{2{\cdot}6} \\
\text{1987:} & \text{Yield} = 6{\cdot}40 \exp - (O_3/0{\cdot}073)^{2{\cdot}3} \\
\text{1988:} & \text{Yield} = 6{\cdot}85 \exp - (O_3/0{\cdot}075)^{2{\cdot}8} \\
\text{Combined years:} & \text{Yield} = 6{\cdot}68 \exp - (O_3/0{\cdot}079)^{2{\cdot}57}
\end{array}
$$

In order to remove year-to-year variations in absolute yield levels caused by differences in meteorological conditions, grain yield was expressed in relative units with the value for the hypothetical maximum yield at 0 μl litre^{-1} O_3 used as the reference (= 1). The exposure–response relationships for the relative yield data are shown in Fig. 3. These relationships were similar in the different years. In 1988, additional stress from strong winds inside the chambers affected the weakened plants in the O_3-2 treatment, which enhanced the effect of O_3 on grain yield.

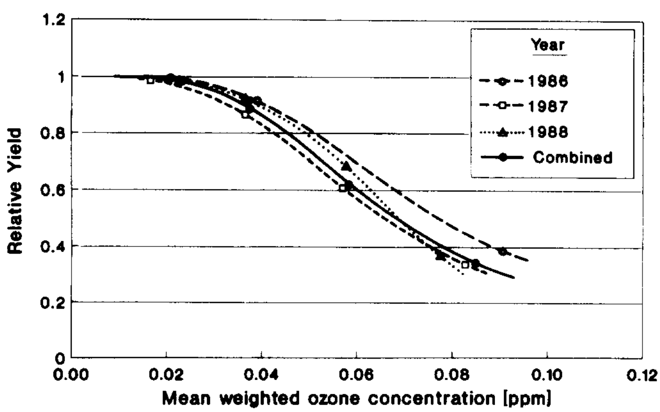

Fig. 3. Exposure–response curves for the relative effect of O_3 on grain yield of spring wheat for individual years and combined years. Curves were produced using the Weibull function.

DISCUSSION

The main objective of this study was to establish a relationship between the O_3 concentration of ambient air and the yield of a field-grown spring wheat cultivar. The relationship obtained at a site located on the Swiss Central Plateau is based upon three experiments carried out in consecutive seasons with either three (1986) or four (1987, 1988) air quality treatments in small open-top chambers. With respect to grain yield, the effects of O_3 observed in the 3 individual years were similar, in spite of differences in climatic conditions. Under the different climatic conditions, the chamber construction either increased or decreased the values for grain yield and other plant characteristics. The relative response of grain yield to increasing O_3, however, remained stable during the 3 years. This agrees with similar observations made in experiments with soybeans in the USA (Heagle *et al.*, 1983, 1987) and preliminary results with spring wheat in Sweden (Pleijel *et al.*, 1988).

In the absence of a large interaction between the climatic conditions and the O_3 response, it seems possible to extrapolate the results obtained inside open-top chambers to ambient field conditions. Nevertheless, one must be cautious regarding extrapolation of the data presented here beyond the conditions of the experiment. It has been identified that important cultivar differences exist with respect to O_3 sensitivity (Heagle *et al.*, 1979; Mulchi *et al.*, 1986; Johnson *et al.*, 1988).

The statistical analysis of the combined data for grain yield from the three experiments reveals a significant treatment effect. The results indicate potential yield losses in spring wheat due to ambient concentrations of O_3 in an important crop-growing area of the country. An increase in O_3 from 0·02 to 0·04 μl litre^{-1} results in a decrease in grain yield of 13%. Effects of similar magnitude have been observed earlier in the USA with sensitive winter wheat cultivars (Kress *et al.*, 1985; Kohut *et al.*, 1987). To our knowledge, the observation of potential yield losses in a field-grown crop reported here is the first made in this country and among the first made in Europe. The extent of the O_3 effect on grain yield and other parameters is very similar to the effect observed with spring wheat in Sweden during the same period of time (Pleijel *et al.*, 1989). The resemblance of the results from this and the Swedish study emphasizes the importance of regional O_3 impacts on agricultural crops in Europe, similar to the importance that was attributed to O_3 in the USA (Heck *et al.*, 1983). However, the results from this study carried out at a site with low concentrations of SO_2 and NO_2, should not be extrapolated to sites with higher concentrations of these gases, since filtration with impregnated filters could reduce the beneficial effect from N and S inputs from the air (Weigel *et al.*, 1987; Fowler *et al.*, 1988). The resulting negative effect could overcome the positive effect from O_3 removal.

On the other hand, at a site with high SO_2 and HF pollution in England, air filtration increased straw and grain yield of spring barley, possibly because of the reduction in phytotoxic HF (Buckenham *et al.*, 1982).

Comparison between the O_3 response of crops observed in different experiments are often made, but it must be remembered that such direct comparisons can be misleading. There are important differences between different experimental protocols, which cause differences in the results. For instance, the length of the fumigation period may differ. In this study, fumigation was carried out from an early growth stage (three to four leaves unfolded) until final harvest. In other studies, fumigation was limited to the period from anthesis until harvest (Amundson *et al.*, 1987), or to the period of pollination (Mulchi *et al.*, 1986). In the absence of O_3 fumigation before anthesis, Amundson *et al.* (1987) observed that reductions in final grain yield were due to reductions in grain size. As observed in the present study and by Kress *et al.* (1985), fumigation with O_3 before, during and after anthesis reduces grain size and grain number, and thus causes larger grain yield reductions. In view of potential effects from ambient O_3 on wheat yield, the timing of episodes with high concentrations in relationship to the developmental stage of the crop is critical.

Another important difference between experiments is the use of different parameters to characterize exposure. In the past, a seasonal 7-h/day or 12-h/day mean O_3 concentration was used in most studies. In the present study, solar radiation-weighted mean concentrations for the period of O_3 fumigation were used, following the suggestion of Rawlings *et al.* (1988). This exposure characterization accounts for daily and seasonal variations in the activity of the plants. While for the CF and NF treatments the difference between calculated 7-h/day or 8-h/day mean concentrations and solar radiation-weighted means is very small, the differences are larger for the O_3-1 and O_3-2 treatments with constant amounts of O_3 added to non-filtered air (data not presented). The use of solar radiation-weighted means as parameter characterizing doses thus affects the parameters of the Weibull function. It appears that by using non-weighted concentrations the O_3 effect may be underestimated. Because of the uncertainties associated with dose parameters, any calculated regression equation must be considered with caution, and in future research emphasis needs to be placed on the evaluation of improved parameters to characterize the O_3 dose during long-term exposures.

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