

## A time–concentration study on the effects of ozone on spring wheat (*Triticum aestivum* L.). 1. Effects on yield

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### Abstract

Spring-sown wheat (*Triticum aestivum* L., cv. 'Promessa') was grown in open-top chambers and ambient-air plots at a site in the southeast of Ireland, and exposed to different concentrations of ozone in a 3-year study carried out from 1991 to 1993. The treatments used in the study were charcoal-filtered air, non-filtered air and non-filtered air to which extra ozone was added. Additional ozone was added to the treatments either as short-term high-concentration exposures or as long-term low-concentration exposures. Air filtration had no significant effect on grain yield, indicating that ambient levels of ozone over the experimental period in the study area did not have the potential to decrease the yield of spring wheat crops. Additional ozone exposures with higher peak concentrations had the most detrimental effect on grain yield. Short-term fumigation with ambient ozone plus 50 parts per billion (p.p.b.) in 1991 resulted in a 53% reduction in grain yield. In 1992 a similar cumulative exposure but with ambient ozone plus 25 p.p.b. applied over a longer time interval increased grain yield by 17%. In 1993 these observations were confirmed when an ozone exposure with higher peak concentrations significantly reduced grain yield, while an identical exposure with lower peak concentrations had no effect. Changes in grain yield were primarily the result of changes in grain filling. They were accompanied by changes in protein percentage as well as in the percentage of small, improperly filled grains. The results suggest that increased emphasis should be given to peak concentrations in the assessment of ozone effects on vegetation.

**Keywords:** Ozone; Spring wheat; *Triticum aestivum* L.; Time–concentration study; Yield

### 1. Introduction

Levels of tropospheric ozone, a photochemical oxidant, have more than doubled in the past one hundred years and are predicted to continue rising at an even faster rate in the future (Hough and Derwent, 1990). The detrimental effects of photochemical oxidant mixtures on plants were first established in the United States in the late 1940s (Middleton et

al., 1950). It has since been established that air pollution by ozone can decrease the yield of agronomically important crops (Heck et al., 1983).

The impact of ozone on wheat yield has been the subject of a number of studies. Reductions in the yield of winter wheat crops because of ambient ozone have been observed in several open-top chamber studies in the United States (Kress et al., 1985; Amundson et al., 1987; Kohut et al., 1987). It has also been demonstrated that ambient levels of ozone may depress the yield of spring wheat crops in Switzerland (Fuhrer et al., 1989), Sweden (Pleijel et al., 1991) and Germany (Adaros et al., 1990).

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Pollutant exposure is commonly represented as a dose, i.e. the pollutant concentration integrated over the time of exposure (Musselman et al., 1986). Inherent in any peak are the two exposure components of concentration and duration (Hogsett et al., 1988). However, increasing evidence shows that plant response is more dependent on the concentration component of the exposure than on the time component. Initial evidence illustrating the importance of concentration in eliciting vegetation effects came from work by Heck et al. (1966). Working with beans and tobacco, they reported that a given exposure distributed over a short period produced more injury than the same exposure distributed over a longer period. Stan et al. (1981) exposed bean plants to different ozone concentrations for varying exposure times and found that stress ethylene production correlated better with ozone concentration than with exposure time when equivalent exposures were compared. Musselman et al. (1983) and Musselman et al. (1986) exposed beans to different ozone concentration distributions and found that the distribution with the highest concentration caused most injury. In a time–concentration experiment, pinto beans were exposed to different concentrations of ozone for different durations in controlled-environment chambers (Maas et al., 1973), and at equivalent ozone exposures peak concentrations were found to be more important than exposure times.

Previous experiments investigating the impact of ozone pollution on wheat yield have, for the most part, used several ozone concentrations applied over the same time interval as treatments (Kress et al., 1985; Mulchi et al., 1986; Amundson et al., 1987; Fuhrer et al., 1989; Adaros et al., 1990; Pleijel et al., 1991). In such experiments only the concentration component of exposure is varied. This study was set up in order to investigate the effects of two components of exposure, time and concentration, on wheat yield.

## 2. Materials and methods

### 2.1. Experimental site

A 3-year experiment was carried out at Oak Park Research Centre, Carlow, Ireland. Carlow lies in the

centre of an intensive tillage area in the southeast of Ireland, and is located about 80 km southwest of Dublin and about 50 m above sea level. Oak Park Research Centre is 4 km due north of Carlow town at latitude 52°51'12" N and longitude 6°54'15" W.

The open-top chambers were located in an open area distant from any local sources or sinks of pollution. An internal farm roadway serves as access to the site. However, it is unlikely that local traffic contributed to air pollution at the site because, on average, fewer than five vehicles per day used the road during the experiments.

### 2.2. Cultural practices

A Dutch-bred cultivar of spring wheat (*Triticum aestivum* L., cv. 'Promessa'), which was on the recommended list of the Irish Department of Agriculture, was used in all 3 years of the experiment. The plots were located in a pasture field. A fine, firm seedbed was prepared after the plots had been dug by tilling with a steel rake followed by compaction with a light roller. Seed was planted by hand in rows 10 cm apart with 5 cm between seeds.

Each crop was fertilised with nitrogen, phosphorus and potassium according to standard agricultural practice. Insecticides and fungicides were applied when necessary in order to keep the crops free from disease (Table 1). The pesticides used had no reported interaction with ozone. Herbicides and growth

Table 1  
Timetable of events during the experiment

Event	1991	1992	1993
Planting	27/4	8/4	28/4
Fertilisation (NPK)	2/4	8/4	28/4
N fertilisation (2nd split)	20/5	13/5	24/5
Fungicide	21/5 <sup>a</sup>	19/5 <sup>b</sup>	7/6 <sup>a</sup>
	18/6 <sup>b</sup>	12/6 <sup>a</sup>	6/7 <sup>b</sup>
	5/7 <sup>a</sup>	10/7 <sup>b</sup>	28/7 <sup>a</sup>
	6/8 <sup>b</sup>		
Insecticide	6/8	19/5	28/6
		12/6	6/7
		10/7	28/7
		17/7	
Final harvest	1/9	19/8	15/9
Start of fumigation	27/5	21/5	21/6
End of fumigation	10/8	31/7	10/8

<sup>a</sup> Fenpropimorph fungicide used. <sup>b</sup> Tebuconazole fungicide used.

regulators were not used during the course of the study. Rodents were controlled by regular application of anti-coagulant rat poison; in addition, ultrasonic rat repellents were used for rodent control during the final year of the study. Slug infestation, particularly at the crop-emergence stage, was controlled using methaldehyde-based molluscicide pellets.

Bird control in the open plots was progressively improved during the 3 years of the study. In 1991 the open plots were unprotected. In 1992 the plots were protected by bird netting at plant canopy level. However, as this measure did not prevent all damage the netting was placed 0.3 m above canopy level in 1993.

Irrigation was carried out when necessary after reference to tensiometers (Model 2725, Soil Moisture Corporation, Santa Barbara, CA, USA) placed centrally in each chamber, so that plots remained close to field capacity. Watering was carried out in a way which negated the effect of rain shadows.

### 2.3. Open-top chambers

The open-top chambers used in the study were modified commercial greenhouses supplied in kit form by Waytorgrow Greenhouses Ltd. (Wickford, Essex, UK). The chambers were 3 m in diameter and 2.8 m tall. Their design incorporated the various recommendations made by Buchenham et al. (1981), which included the presence of an internal collar situated 2.3 m above ground level at the eaves of the chamber and a frustrum, a lip on top of the chambers

sloping inwards. These additions are designed to reduce incursions of ambient air into the chambers.

Air was blown into the chambers continuously from fans (Model No. EK31, Radial Axial Ltd., Hertfordshire, UK) through a circular perforated annulus situated just above the crop canopy. The flow rate corresponded to approximately three air exchanges per minute. Air filtration was achieved by passing the ambient air through a number of layers of activated charcoal.

### 2.4. Treatments

Two treatments were common to all years: (1) open plots (ambient-air plots without chambers); (2) filtered (chambers with charcoal-filtered air). Non-filtered treatments were used during the first 2 years of the study. Table 2 summarises the fumigation treatments used in the course of the study. During 1991 a further treatment (A + 50) received ambient concentrations of ozone plus 50 parts per billion (p.p.b.) supplied 4 h a day for 4 days a week. In 1992 a fourth treatment (A + 25) received ambient concentrations of ozone plus 25 p.p.b. supplied 6 h a day for 5 days a week. In 1993 the A + 25 treatment received ambient ozone plus 25 p.p.b. supplied 6 h a day for 5 days a week, and the A + 50 treatment received ambient ozone plus 50 p.p.b. supplied 3 h a day for 5 days a week. **Each treatment was replicated three times.** The exposure regimes were chosen to represent different combinations of time and concentration for identical cumulative exposures in order that the effect of these combinations on the yield of spring wheat could be assessed.

Table 2  
Fumigation treatments used in this study

Year	Treatment	Concentration	Duration	Start date	Finish date
1991	A + 50	Ambient + 50 p.p.b.	4 h day <sup>-1</sup> 4 days week <sup>-1</sup>	27 May	10 August
1992	A + 25	Ambient + 25 p.p.b.	6 h day <sup>-1</sup> 5 days week <sup>-1</sup>	21 May	31 July
1993	A + 25	Ambient + 25 p.p.b.	6 h day <sup>-1</sup> 5 days week <sup>-1</sup>	21 June	10 August
1993	A + 50	Ambient + 50 p.p.b.	3 h day <sup>-1</sup> 5 days week <sup>-1</sup>	21 June	10 August

Table 3  
Climate data: April to August

	Sunshine (h)	Rainfall (mm)	Average maximum temperature (°C)	No. of days with maximum temperature > 20°C
1991	680.1	266.1	17.1	43
1992	707.6	298.3	17.9	49
1993	594.4	404.9	16.9	25

### 2.5. Pollutant generation and distribution

Ozone was generated from a feedstock of ordinary grade oxygen (Irish Industrial Gases, Dublin) by silent electric discharge (Ozone Generator, Model No. LN-103, Asea Brown Boveri Ltd., Baden, Switzerland). During the first 2 years of the study ozone-enriched air from the ozone generator was distributed to the chambers via a manifold, and 6.4 mm outside diameter (OD) Teflon tubing. Ozone concentrations in individual chambers could be adjusted by controlling flow rates using needle valves.

During the final year of the study ozone-enriched air from the ozone generator was first divided between two stainless steel manifolds, one for each fumigated treatment, before being distributed to the chambers via 6.4 mm OD Norprene tubing, an oxidant-resistant material. Flow-rate adjustment by ro-

tameters allowed ozone concentrations in individual chambers to be controlled.

### 2.6. Pollutant and climate monitoring

Ozone concentrations were monitored using a UV absorption analyser (Model No. 8810, Monitor Labs Inc., San Diego, CA, USA). Ambient air was sampled at a point 6 m above ground level and drawn into the analyser through 6.4 mm OD Teflon tubing by means of a teflon membrane pump (Model No. N.726, KNF Neuberger, Oxford, UK). Ambient ozone concentrations were recorded twice hourly using a data logger (Campbell Scientific 21x). Ozone concentrations in each of the fumigated chambers were monitored manually at least once every half hour. Air in the chambers was sampled at plant canopy level at a point midway between the centre of the chamber and the chamber walls. Climate data were obtained from an official climatological station located immediately adjacent to the site.

### 2.7. Final harvest

Once the crops had ripened four quadrats, containing 18 plants, were harvested from points near the centre of each plot. The number of ears per plant was determined, and the ears and straw were sepa-

Table 4  
Seasonal mean ozone concentrations in the different treatments

Year	Treatment	24 h mean	12 h total <sup>a</sup> (09:00–21:00 h, GMT + 1) in p.p.b.–hours	90th percentile
1991	Ambient air	20.2	24 909.9	26.8
	Filtered	4.6	5 601.1	6.2
	Non-filtered	20.2	24 909.9	26.8
	Ambient + 50	22.7	32 614.1	40.9
1992	Ambient air	18.4	25 098.7	24.4
	Filtered	4.2	6 230.9	5.6
	Non-filtered	18.4	25 098.7	24.4
	Ambient + 25	21.4	33 418.6	35.4
1993	Ambient air	21.2	29 177.7	29.2
	Filtered	4.8	6 700.2	6.7
	Ambient + 25	23.1	33 987.5	36.4
	Ambient + 50	23.1	34 004.0	39.0

<sup>a</sup> Calculated between 1 May and 10 August.

rated and weighed. The ears from each quadrat were carefully threshed using a head thresher (Type LD 180, Walter and Wintersteiger, Austria). The protein content of the grain was determined by combustion (LECO FP-228, LECO Corporation, St. Joseph's, MI, USA).

The remaining plants in each chamber were also harvested and threshed. Grain from this bulk harvest was used to determine the following parameters: thousand grain weight, hectolitre weight (weight per volume) and percentage screenings (small, improperly filled grains). The percentages of dry matter in grain and straw were determined by drying samples from the bulk harvest at 100°C to constant weight. Harvest index, a parameter which describes the partitioning of dry matter between grain and straw, was calculated as the percentage grain weight in total dry weight.

## 2.8. Statistics

Replicate chamber means were calculated as the mean of the results from the four chamber quadrats.

Single-way analysis of variance was used to determine differences among treatments using the Minitab statistics package. Means are presented with standard errors.

## 3. Results

### 3.1. Climatic conditions and ozone concentrations

Table 3 shows seasonal values of sunshine hours, rainfall and temperature for the 3 years of the study. Climatic conditions in 1991 and 1992 were similar, but 1993 was colder and wetter with lower levels of sunshine.

Table 4 shows 24 h seasonal mean ozone concentrations for the different treatments. Seasonal means were calculated for the months of May, June and July, months coinciding with the crop phenological stages most sensitive to ozone. Table 4 also shows average 90th percentile values as well as seasonal 12 h totals for the different treatments, as these parameters offer an alternative description of the nature of

Table 5

Mean values of straw yield, grain yield and grain yield components for spring wheat in the different treatments

Year	Treatment	Dry wt. grain per plant (g)	Dry wt. straw per plant (g)	Thousand grain weight (g)	No. of ears per plant (g)	No. of ears per m <sup>2</sup>	No. of grains per ear
1991	Filtered	4.04 ± 0.34	2.27 ± 0.18	51.66 ± 0.88	2.39 ± 0.13	337.25 ± 16.91	38.33 ± 0.57
	Non-filtered	4.19 ± 0.64	2.39 ± 0.31	50.66 ± 0.33	2.41 ± 0.27	312.61 ± 21.83	39.98 ± 1.39
	Ambient + 50 p.p.b.	1.88 ± 0.08 ***	1.87 ± 0.15	33.33 ± 1.33 ****	2.17 ± 0.16	309.96 ± 9.81	30.19 ± 0.94 ****
	Open plot	1.87 ± 0.31 ***	1.97 ± 0.35	52.66 ± 0.33	1.56 ± 0.22 **	268.22 ± 31.85	27.43 ± 1.07 ****
	Filtered	3.22 ± 0.25	1.82 ± 0.11	47.33 ± 2.33	2.10 ± 0.11	278.96 ± 24.96	38.33 ± 2.91
1992	Non-filtered	3.32 ± 0.23	1.91 ± 0.10	46.66 ± 1.20	2.10 ± 0.17	275.63 ± 23.38	40.23 ± 1.46
	Ambient + 25 p.p.b.	3.78 ± 0.30 #	2.37 ± 0.28 ##	52.0 ± 0.58	2.34 ± 0.20	330.8 ± 27.03	38.10 ± 0.57
	Open plot	2.55 ± 0.09 +	2.35 ± 0.11 +	51.33 ± 2.40	2.34 ± 0.04	291.47 ± 12.99	32.33 ± 1.31 **
1993	Filtered	4.05 ± 0.09	2.41 ± 0.08	54.66 ± 0.88	2.38 ± 0.08	423.06 ± 20.55	36.82 ± 1.38
	Ambient + 25 p.p.b.	3.92 ± 0.12 ††	2.45 ± 0.17	50.66 ± 1.45	2.48 ± 0.14 †	454.46 ± 42.34	35.76 ± 0.88
	Ambient + 50 p.p.b.	3.37 ± 0.28 **	2.19 ± 0.09	47.33 ± 2.96 **	2.22 ± 0.06	406.56 ± 13.53	37.98 ± 0.42
	Open plot	3.75 ± 0.09	2.53 ± 0.10	52.66 ± 0.88	2.09 ± 0.08 +	334.13 ± 7.38	40.21 ± 0.38 ††
	Filtered	3.22 ± 0.25	1.82 ± 0.11	47.33 ± 2.33	2.10 ± 0.11	278.96 ± 24.96	38.33 ± 2.91

Significant difference between filtered and A + 50: \*  $P < 0.1$ ; \*\*  $P < 0.05$ ; \*\*\*  $P < 0.01$ ; \*\*\*\*  $P < 0.001$ .

Significant difference between filtered and A + 25: #  $P < 0.1$ ; ##  $P < 0.05$ . Significant difference between unfiltered and open plot: +  $P < 0.1$ ; ++  $P < 0.05$ ; +++  $P < 0.01$ ; ++++  $P < 0.001$ .

Note: In 1993 open plots were compared statistically with filtered plots.

Significant difference between A + 50 and A + 25: †  $P < 0.1$ ; ††  $P < 0.05$ .

the treatments. Results presented for non-filtered and filtered treatments are based on ambient air data and knowledge of filtration efficiency. Concentrations of ozone in ambient air were similar in all 3 years of the study.

### 3.2. Effects on grain yield

Tables 5 and 6 give yield measurements from the 3 years of the study. Improvements in bird control led progressively to better yields from the open plots over the 3 years. As a result of excessive bird damage during the first 2 years, a chamber-effects comparison was not made for these 2 years of the study. Air filtration had no significant effect on any of the parameters measured at the final harvest in either 1991 or 1992.

In 1991, fumigation with ambient ozone plus 50 p.p.b. caused a 53% reduction in the dry weight of grain per plant ( $p < 0.01$ ) compared with that from the filtered treatment. Although the dry weight of straw was also apparently reduced by this treatment, the effect was not significant. Reduction in grain weight was primarily associated with reduction in grain filling ( $p < 0.001$ ) and, to a lesser extent, with reductions in the number of grains per ear ( $p < 0.001$ ). This treatment had no significant effect on the number of ears per unit ground area.

In 1992 the fumigation treatment had a similar total exposure to that of 1991 (Table 4), but was applied as a lower concentration over a longer time interval. This treatment resulted in significant increases in the dry weight of grain ( $p < 0.1$ ) and in the dry weight of straw per plant ( $p < 0.05$ ). The increase in grain yield was associated with a greater thousand grain weight and a larger number of ears per square metre, although the differences were not significant. The treatment had no significant effect on the number of grains per ear.

In 1993, treatments similar to those employed in the first 2 years of the study were used. The A + 25 treatment had no significant effect on the yield of grain or straw in comparison with the filtered treatment, but the A + 50 treatment caused a significant reduction in the dry weight of grain per plant ( $p < 0.05$ ). The dry weight of straw per plant was not affected. The reduction in grain weight was primarily the result of a negative effect on grain filling ( $p < 0.05$ ), as no significant reductions in the number of grains per ear or in the number of ears per plant were recorded.

There was little difference in harvest index among chamber treatments in 1992 and 1993. However, in 1991 the A + 50 treatment caused a significant reduction ( $p < 0.001$ ) in harvest index. Ozone treatment resulted in changes in the percentage screen-

Table 6

Mean values of harvest index, hectolitre weight, percentage screenings and percentage protein for spring wheat in the different treatments

Year	Treatment	Harvest index	Hectolitre weight (Kg HL <sup>-1</sup> )	Percentage screenings	Percentage protein
1991	Filtered	0.63 ± 0.00	83.33 ± 0.22	2.07 ± 0.23	9.68 ± 0.38
	Non-filtered	0.63 ± 0.00	83.1 ± 0.25	3.46 ± 0.07	9.09 ± 0.39
	Ambient + 50 p.p.b.	0.50 ± 0.01 ****	76.65 ± 0.22 ****	10.89 ± 1.64 ****	11.70 ± 0.34 ***
	Open plot	0.50 ± 0.02 + + + +	82.33 ± 0.54 + +	1.18 ± 0.27 +	7.31 ± 0.22 + + +
1992	Filtered	0.63 ± 0.00	81.16 ± 0.34	1.51 ± 0.36	9.41 ± 0.09
	Non-filtered	0.63 ± 0.00	81.36 ± 0.34	1.56 ± 0.13	9.29 ± 0.28
	Ambient + 25 p.p.b.	0.61 ± 0.00	78.96 ± 1.33	0.59 ± 0.08 ###	8.88 ± 0.17 #
	Open plot	0.55 ± 0.00 + + + +	73.93 ± 1.89 + + +	0.35 ± 0.05 ***	6.69 ± 0.15 + + + +
1993	Filtered	0.62 ± 0.00	81.69 ± 0.49	0.96 ± 0.01	9.54 ± 0.40
	Ambient + 25 p.p.b.	0.61 ± 0.01	76.86 ± 2.07	0.78 ± 0.21 †	9.92 ± 0.23
	Ambient + 50 p.p.b.	0.60 ± 0.01	75.54 ± 3.00 *	1.44 ± 0.31	9.42 ± 0.24
	Open plot	0.59 ± 0.00 +	81.44 ± 0.93	0.80 ± 0.23	7.92 ± 0.24 + + +

Significant difference between filtered and A + 50: \*  $P < 0.1$ ; \*\*  $P < 0.05$ ; \*\*\*  $P < 0.01$ ; \*\*\*\*  $P < 0.001$ .

Significant difference between filtered and A + 25: #  $P < 0.1$ ; ##  $P < 0.05$ ; ###  $P < 0.01$ .

Significant difference between open plot and unfiltered: +  $P < 0.1$ ; + +  $P < 0.05$ ; + + +  $P < 0.01$ ; + + + +  $P < 0.001$ .

Note: In 1993 open plots were compared statistically with filtered plots.

Significant difference between A + 50 and A + 25: †  $P < 0.1$ ; ††  $P < 0.05$ .

ings and thousand grain weights. Grain from the A + 50 treatment in 1991 had a low thousand grain weight and high percentage screenings ( $p < 0.001$ ). In 1992 a high thousand grain weight from the A + 25 treatment was accompanied by low percentage screenings ( $p < 0.01$ ). The A + 50 treatment had no significant effect on percentage screenings in 1993. Hectolitre weight (weight of grain per volume) was significantly reduced ( $p < 0.001$ ) by the A + 50 treatment in 1991 and again in 1993 ( $p < 0.1$ ). The A + 25 treatment in 1992 had no significant effect on this parameter. In 1991 the A + 50 treatment caused a significant increase ( $p < 0.01$ ) in the percentage protein in grain, and the A + 25 treatment in 1992 significantly decreased ( $p < 0.1$ ) percentage protein.

#### 4. Discussion

This study demonstrates that for equal cumulative exposures, short-term high-concentration exposures are considerably more phytotoxic than long-term low-concentration exposures. In 1992 an ozone treatment with similar cumulative exposure but a different concentration distribution to that applied in 1991 reversed the effect of ozone found the previous year, stimulating yield rather than reducing it. This comparison between 1991 and 1992 only considers the difference in fumigation regimes and neglects the possibility that there may have been an interaction between the effect of ozone and the prevailing climatic conditions. However, two previous open-top chamber studies have shown that climatic conditions have no effect on the relative response of spring wheat to ozone (Fuhrer et al., 1989; Pleijel et al., 1991). In any case, in 1993 the results of the previous 2 years were confirmed when an ozone exposure with higher peak concentrations significantly reduced grain yield, while an identical ozone exposure with lower peak concentrations had no effect. This result agrees with similar observations made in time–concentration experiments conducted with indoor fumigations (Heck et al., 1966; Maas et al., 1973).

The reductions in grain yield which resulted from ozone treatment were primarily attributable to reductions in grain filling, as measured by the thousand

grain weight, and secondarily to reductions in the number of grains per ear. Similar results have been reported from other studies with wheat (Kress et al., 1985; Kohut et al., 1987; Fuhrer et al., 1989; Fuhrer et al., 1992). In other experiments reductions in yield which were entirely attributable to reductions in seed weight have been reported, but in those studies the ozone fumigation commenced at anthesis (Amundson et al., 1987; Pleijel et al., 1991). The timing of the start of ozone fumigation is thus important in determining which of the yield components are affected by ozone treatment. Hence, it is possible that the late commencement of fumigation in 1993 prevented the A + 50 treatment of that year having a detrimental effect on the number of grains per ear.

In 1991 fumigation with high ozone concentrations altered the partitioning of dry matter between grain and straw. In this case relatively more dry matter was partitioned to straw than to grain. Decreases in harvest index have also been reported in other studies on the effects of ozone on wheat (Mulchi et al., 1986; Fuhrer et al., 1989; Pleijel et al., 1991; Fuhrer et al., 1992). However, in 1992 and 1993 the fumigated treatments had no significant effect on harvest index, indicating that changes in grain weight were accompanied by similar changes in straw weight. Changes in the allocation of carbohydrate typically lead to proportional changes in the concentrations of other grain constituents. As protein is laid down in the aleurone layer and embryo before the start of grain filling, a reduction in carbohydrate supply has the effect of increasing the percentage protein in grain. This is the most likely mechanism by which the A + 50 treatment in 1991 increased the percentage protein in the grain. Increases in protein content have also been observed in other wheat studies (Fuhrer et al., 1990; Pleijel et al., 1991; Fuhrer et al., 1992). Conversely, the reduction in percentage protein caused by the A + 25 treatment in 1992 was more than likely a consequence of the increased grain fill diluting the protein present in the grain.

Increases in grain yield in response to sub-toxic levels of ozone as, found in 1992, have also been reported in studies on the effects of ozone on spring wheat (Adaros et al., 1990) and on winter wheat (Kress et al., 1985). Positive effects of low ozone treatments have also been found in soybeans (En-



dress and Grunwald, 1985) and pumpkins (Rajput and Ormrod, 1986), as well as in field beans (Sanders et al., 1992). Adaros et al. (1990) suggested that such results may reflect that plants have already adapted their growth to high ambient levels of ozone.

Air filtration had no significant effect on grain yield during the first 2 years of the study, indicating that ambient levels of ozone in the southeast of Ireland were not high enough to cause yield reductions in spring wheat. The presence of low levels of air pollutants is not surprising in view of the fact that Ireland has a low level of industrialisation and vehicle emissions compared with many of its European neighbours. Ireland lies on the fringe of Europe, where the prevailing winds are from a westerly direction. Only occasionally do winds blow from continental Europe, a region with substantially higher levels of air pollutants (Fowler et al., 1992).

This study, which the authors believe to be the first of its kind on wheat, clearly demonstrates the importance of peak concentrations in ozone damage. Peak concentrations probably cause greater damage because the greater the amount of absorbed pollutant, the more likely it is that the toxicant will exceed the plant's ability to compensate for it (Hogsett et al., 1988). A major implication of this result is that increased emphasis must be given to high concentrations in the assessment of ozone effects on vegetation. This aspect is considered in more detail in a subsequent paper (Finnan et al., 1996).

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