Effects of Open-Air Fumigation with Sulphur Dioxide on the Occurrence of Fungal Pathogens in Winter Cereals

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ABSTRACT

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An open-air fumigation system was constructed to determine the effects of sulphur dioxide on the growth and yield of winter cereals. Winter barley (*Hordeum vulgare*) cultivar Sonja was grown during 1982–1983 and winter wheat (*Triticum aestivum*) cultivar Rapier during 1983–1984. This paper describes the occurrence of the pathogens *Puccinia hordei, Rhynchosporium secalis*, and *Pseudocercosporella herpotrichoides* on barley and *Erisyphe graminis, P. herpotrichoides*, and *Fusarium* spp. on wheat at four sulphur dioxide concentrations in the range 0.01–0.06 ppm. The crops were exposed to elevated levels of sulphur dioxide in 30-m-diameter field plots from shortly after emergence in autumn until maturity during the following summer. Interactions were observed between the levels of disease infestation and exposure to sulphur dioxide. The magnitude of the SO_2-pathogen interactions at ambient concentrations and under field conditions suggests that these have considerable importance for plant growth and requirements for disease control measures that may not be apparent from air pollution studies using conventional exposure chambers.

Additional key words: air pollution, brown foot rot, brown rust, eyespot, leaf blotch, powdery mildew.

The effects of atmospheric sulphur dioxide (SO_2) on the production of crops have been the subject of numerous investigations (23). Early experimental work was often performed in closed laboratory or greenhouse chambers (14,30) in which environmental conditions might have been atypical of field conditions or at concentrations in excess of ambient levels. Recent studies have utilized open-top field chambers in which a more natural environment is maintained (12,20,31). However, minimal alteration of environmental conditions is only achieved using air exclusion systems (25,39) and open-air fumigation systems (11,28,29,33,36), which use field plots without any form of enclosure. It is then possible to observe any interaction of the air pollutant treatment with the natural occurrence of other environmental factors such as drought, cold (11), and disease.

A new open-air fumigation system was designed and constructed to expose cereal crops to controlled concentrations of SO_2 (33). The objective of the experiments was to simulate ambient exposures of crops to a range of fluctuating SO_2 concentrations, which included values typical of U.K. conditions, and to evaluate the effects on crop growth. This paper reports observations of fungal pathogens that occurred naturally in two fumigated cereal crops and considers their importance for crop growth and experimental techniques used in air pollution studies.

MATERIALS AND METHODS

The study was conducted in a 2-ha experimental field situated at the Glasshouse Crops Research Institute, Littlehampton, West Sussex, UK (Lat. 50°49′N, Long. 0°31′W). The site is 2.5 km from the south coast on the Sussex coastal plain on a Brickearth soil of the Hamble series (22).

Shortly after crop emergence the dispersion pipework of the fumigation system was placed in position on the soil surface. The details of the system design and principles of operation have been described (35). The system was designed to achieve uniformity of hourly-mean SO_2 concentration across a 9-m-diameter area in the center of each plot during the most frequent conditions of atmospheric stability (34). The horizontal distribution of hourly mean concentration was not routinely monitored but was found to vary by less than 5% during a detailed investigation (33). Three experimental plots were treated with SO_2, and a fourth contained dispersion pipework but received no treatment and was exposed only to background SO_2. Two 9-m-diameter companion control plots, without pipework, were located 30 m to the east and to the west of each piped plot, thus permitting comparisons of a treated plot with adjacent controls to reduce any confounding natural variation in yield observed across the experimental field.

The concentration of SO_2 was measured at the center of each plot with a Meloy SA285E flame photometric sulphur dioxide analyser (Meloy Laboratories Inc.), and the release rate of SO_2 was

controlled by a computer connected to electronic mass flow valves to maintain a sequence of hourly mean target concentrations. These target concentrations were taken from measurements at Bottesford, a rural site 20 km from towns and industrial sources in central England (32) and stored as a sequence within the control computer. These concentrations were used directly as the target values for the lowest treatment but were increased by adding a further 0.03 and 0.06 ppm of SO_2 for the medium and high treatments. Exposure to SO_2 was continuous except when the gas supply was automatically turned off at wind velocities below 1 m s^{-1}, which occurred for 20% of the experimental periods (33). Equipment faults and calibration also prevented fumigation for 3% of the time. Subject to the limitation of low wind velocity, the gas release continued during rainfall and when the vegetation was covered with dew. A Dasibi Model 1003 PC O_3 analyzer (Dasibi Environmental Corp., Glendale, CA) was used to monitor background O_3 and a Monitor Labs Model 8840 (Monitor Labs, Inc., San Diego, CA) to monitor background NO and NO_2. Data on rainfall, temperature, relative humidity, and total solar radiation were available from a meteorological station located 0.5 km from the site (4,7,9).

Winter barley. Winter barley (*Hordeum vulgare* L.) cultivar Sonja was grown during 1982–1983 and winter wheat (*Triticum aestivum* L.) cultivar Rapier during 1983–1984. The barley crop was drilled on 10 September 1982, seed rate 220 kg ha^{-1}, and received an application of preemergent herbicide, 3.5 kg ha^{-1} of chlortoluron (3-(3-chloro-*p*-tolyl)-1,1-dimethylurea), and fertilizer (250 kg ha^{-1}, NPK ratio 5:20:25). Throughout the experiments the normal agricultural practices for cultivation in the area were followed. Fumigation with SO_2 commenced on 1 November 1982 and terminated on 5 July 1983. On 5 November, the field was sprayed with 125 g ha^{-1} of triadimefon (1-[4-chlorophenoxy]-3,3-dimethyl-1-[1*H*-1,2,4-triazol-1-yl]butanone) as a precautionary autumn fungicide treatment against mildew (*Erisyphe graminis* DC. ex Mérat f. sp. *hordei* Em. Marchal) and an insecticide, 140 g ha^{-1} of pirimicarb (2-dimethylamino-5,6-dimethylpyrimidin-4-yl dimethylcarbamate), to reduce the potential for aphid transfer of barley yellow dwarf virus.

Brown rust (*Puccinia hordei* Otth) was observed throughout the field and was assessed on two occasions within the piped plots using assessment keys (1,24). As a preliminary assessment, on 8 March 10 randomly selected tillers were taken from the background and highest treatment plots, and each living leaf was examined for the percentage of leaf area affected by rust pustules. As levels of infestation were low on some leaves, interpolations between standard assessment diagrams (24) were made to include a category of 0.1% leaf area affected (two pustules per leaf) and 0.5% leaf area affected (10 pustules per leaf). These leaf samples were also analyzed for their content of N, P, K, Mg, Ca, and S. On 10 March, brown rust was reassessed on the five youngest fully developed leaves of 25 plants, which were sampled by taking five plants from five random locations within each piped plot. Infected leaves showed less than 5% leaf area occupied by pustules, and the disease was assessed by scoring presence or absence of pustules on each leaf. The leaves were simultaneously examined for the presence or absence of lesions of *Rhynchosporium secalis* (Oud.) J. J. Davis, and each plant was examined for the presence or absence of stem lesions of *Pseudocercosporella herpotrichoides* (Fron) Deighton. On 16 April, there was a planned application of fertilizer (440 kg ha^{-1}, 33% N) and on 29 April 125 g ha^{-1} of triadimefon was applied, as would be a normal practice to control a rust infestation of this magnitude.

As part of a routine assessment of crop growth, five replicate samples comprising all plants in four adjacent 0.5-m row lengths were removed at 4–5 wk intervals from each treatment and companion plot for examination. The number of plants and number of tillers per plant were counted, and the live leaf material was separated. Leaf area was determined on a 15% subsample of leaf material using a Model 528 Area Quantifier (KGM Vidiaids Ltd., Middlesex, U.K.). The aboveground stem, leaf, and leaf subsample were oven-dried at 80 C for dry weight determination. Sample leaf area index was calculated from the area:weight ratio of the subsample.

Winter wheat. The wheat crop was drilled on 1 October 1983 at a seed rate of 188 kg ha^{-1} with an application of fertilizer (250 kg ha^{-1}, NPK ratio 5:20:25). Before drilling, the field received an application of 200 kg ha^{-1} of unscreened ground chalk. On 6 October, 2.5 kg ha^{-1} of chlorsulfuron (1-[2-chlorophenylsulphonyl]-3-[4-methoxy-6-methyl-1,3,5-triazin-2-yl]urea) and methabenzthiazuron (1-[benzothiazol-2-yl]-1,3-dimethylurea) was applied as a preemergent herbicide, and on 31 October a routine insecticide treatment of 244 g ha^{-1} of demeton-S-methyl (5-2-ethylthioethyl *O,O*-dimethyl phosphorothioate) and fungicide, 125 g ha^{-1} of triadimefon, were applied. Fumigation with SO_2 commenced on 3 November 1983 and terminated on 7 August 1984. A topdressing of fertilizer was given on 17 February 1984 (188 kg ha^{-1}, 33% N) and on 18 April 1984 (250 kg ha^{-1}, 33% N). Because of high levels of infestation of wheat by *Septoria tritici* Rob. in Desm. in the county, a precautionary fungicide application of 125 g ha^{-1} of propiconazole (1-[[2-[2,4-dichlorophenyl]-4-propyl-1, 3-dioxolan-2-yl]methyl]-1*H*-1,2,4-triazol) was made on 15 June 1984.

Levels of powdery mildew (*E. g.* f. sp. *tritici* E. Marchal) were assessed on three occasions: 5, 14, and 27 June 1984 in piped plots only. Twenty-five randomly selected tillers were taken from each plot, and the percentage of leaf area occupied by pustules was assessed on all leaves of each tiller using assessment keys (1,24). Twenty-five tillers were also assessed for *P. herpotrichoides* and *Fusarium* spp. on 16 and 24 July 1984. *P. herpotrichoides* was scored as the presence or absence of characteristic lesions at the stem base. The two lowest nodes of each stem base were separately scored for the presence of the characteristic stem blackening of *Fusarium*, and the presence of pink pustules (2) at either node was also noted. Samples of the crop were taken for determination of crop dry weight and leaf area index as described above. The wheat crop was harvested on 8 August 1984.

RESULTS

Environmental conditions. The growing season 1982–1983 was marked by a particularly wet and mild autumn with twice the average rainfall in October including long periods of continuous rain. February was dry and sunny followed by a cold, dull, and particularly wet spring with twice the average rainfall in April and May. These conditions were accompanied by the appearance of brown rust (*P. hordei*) in most winter barley crops (6) and the occurrence of leaf blotch (*R. secalis*) in most barley crops in the south of England, occasionally reaching severe levels (5). The summer months of June and July were mainly warm, dry, and sunny.

The 1983–1984 season began with a dry autumn, 46% below average rainfall in November, a warm, wet winter, followed by alternating months of above and below average rainfall, including a particularly dry April with $<2\%$ average rainfall accompanied by sunny weather. The subsequent heavy rainfalls in May led to a high risk of cereal disease development with *S. tritici* and *E. graminis* affecting most crops in the southeast of England in June (8).

The arithmetic mean concentrations of SO_2 obtained over the duration of the experiments were 0.010, 0.023, 0.038, and 0.058 ppm during 1982–1983 and 0.011, 0.024, 0.046, and 0.057 ppm during 1983–1984 (Table 1). The SO_2 exposure was subject to fluctuations caused by changes in wind velocity, wind direction, and atmospheric dispersion throughout the experiment. Consequently, the mean does not adequately characterize the exposure (36). As the extremes of concentration may be an important component of exposure, the concentrations exceeded for 50, 5, and 1% of the time are also provided. Mean background concentrations of O_3, NO, and NO_2 were found to be low at 0.020 ppm of O_3, 0.003 ppm of NO, and 0.012 ppm of NO_2 in each year (Table 1).

Winter barley. After the application of a routine autumn fungicide treatment on 5 November, the plants appeared healthy and had reached growth stage 26 by 15 January (43). On 24 February, older leaves throughout the entire crop began to yellow

TABLE 1. Characteristics of the SO_2 exposure by open-air fumigation of winter barley November 1982–July 1983 and winter wheat November 1983–July 1984

Year	Plot	Arithmetic mean (ppm)	Standard deviation	Percentile concentration (ppm)[a] 50%	5%	1%	Maximum hourly mean
1982–1983							
	Background	0.010	0.013	0.005	0.034	0.059	0.122
	Low	0.023	0.023	0.017	0.070	0.102	0.219
	Medium	0.038	0.028	0.039	0.084	0.117	0.300
	High	0.058	0.043	0.065	0.116	0.158	0.440
	O_3	0.020	0.013	0.020	0.040	0.053	0.086
	NO	0.003	0.009	0.001	0.013	0.050	0.140
	NO_2	0.011	0.010	0.008	0.032	0.046	0.075
1983–1984							
	Background	0.011	0.012	0.007	0.034	0.057	0.171
	Low	0.024	0.021	0.020	0.061	0.095	0.240
	Medium	0.046	0.039	0.045	0.098	0.160	0.500
	High	0.057	0.044	0.062	0.111	0.195	0.510
	O_3	0.020	0.016	0.020	0.042	0.065	0.101
	NO	0.003	0.011	0.001	0.019	0.059	0.128
	NO_2	0.012	0.011	0.009	0.026	0.048	0.072

[a] The hourly mean concentration that is exceeded for the respective percentage of time.

TABLE 2. Percentage of leaf area of winter barley affected by brown rust *Puccinia hordei* sampled on 8 March 1983 from a plot exposed to SO_2 and a background plot[a]

SO_2 Treatment	Leaf number 5	4	3	2	1
High	Dead	0	0	0	0
Background	Dead	4.6	2.6	0.2	0

[a] Values shown are the mean percentage for each leaf from 10 randomly selected tillers.

except in areas exposed to SO_2, which remained green. Plants receiving the highest concentration were distinctly different in color, but only a slight difference was visible between plants receiving lowest SO_2 concentrations and the remainder of the field.

On 8 March, *P. hordei* was identified on many leaves outside the SO_2 treated plots, and the disease level was assessed as described (Table 2). This revealed no disease on the leaves of plants exposed to the highest level of SO_2. On plants exposed to background SO_2, 5% of the surface area of the oldest living leaves (leaf no. 4) was covered with rust pustules. Analysis of leaf material for N, P, K, Mg, Ca, and S revealed no apparent nutrient deficiencies of these plants. The total S content of leaves from both plots was 0.3% (J. Fletcher, *unpublished data*).

On 10 March 1983, *P. hordei* was reassessed and the amount of *R. secalis* and *P. herpotrichoides* was determined (Fig. 1). Rust pustules occupied less than 5% of the area of the five youngest leaves, and presence or absence within this range was scored. Older leaves generally showed higher levels of rust (5–10% of the leaf area). The data for each species were examined using the Kolmogorov-Smirnov test as a measure of population similarity (13). The frequency of rust-infected leaves in samples from treated plots was compared with that from the background plot (Fig. 1B). In each case the distribution of infected leaves is dissimilar ($p < 0.01$), suggesting that all SO_2 treatments had modified the level of disease infestation. The frequency of leaf infestation by *R. secalis* was also significantly different between each treated plot and the background plot ($p < 0.01$), suggesting that both foliar diseases decreased with increasing SO_2 concentration.

The level of infestation by *P. herpotrichoides* increased in the low and medium SO_2 plots compared with the background plot but was reduced in the high SO_2 plot compared with the medium plot (Fig. 1A). Analysis of the number of infected and uninfected samples using the chi-square test (13) revealed no significant differences between the control, low, and high plots. However, the medium plot had a significantly higher infection than the control plot ($p < 0.001$).

During the period of rust infestation, measurements of leaf area index on 16 March revealed significantly larger leaf areas in medium and high SO_2 treated plants (Table 3). This difference in plant growth was readily apparent with visual observation and was caused by the yellowing and death of rust-infested leaves in unfumigated plots. Subsequent measurements on 27 April showed that growth differences were also manifested as significant increases in the dry weight of plants receiving the low and medium SO_2 treatment. Following these measurements, a fungicide was applied on 29 April to control the rust infestation. At final harvest the differences in dry weight were no longer significant. However, the crop had developed symptoms of barley yellow dwarf virus (BYDV), which resulted in considerable variability in plant performance. Twenty tillers sampled from each treatment plot in June were 95–100% infected with BYDV (J. Fletcher, *unpublished data*), and there was no interaction between BYDV and SO_2 treatment.

Winter wheat. There were no major outbreaks of pathogens during the cultivation of the wheat crop. Small amounts of *E. graminis* were observed on leaves in December 1983 and isolated samples of *Rhizoctonia cerealis* van der Hoeven, *P. herpotrichoides*, and *Fusarium* spp. on stems between March and June 1984. Leaf spot caused by *S. tritici* was observed on some plants during May. On 17 April a few mildew pustules were detectable on the lower leaves of all plants, which increased in extent on the lower leaves and stems of plants exposed to the highest SO_2 treatment by 31 May. Assessment of the level of mildew infestation was performed on 5 June, when ears were emerging from the leaf sheath at growth stage 50–55 (43) and again on 14 and 27 June (Fig. 2). On 27 June there were only four living leaves remaining on all tillers sampled. The level of mildew infestation was always greater at the base of the plant canopy (leaf 5, Fig. 2) and increased more rapidly to reach the highest level in the high SO_2 plot. The proportion of leaves infected, uninfected, or dead was examined using the Kolmogorov-Smirnov test (13) for each leaf position on each sampling date. On all occasions there were significant differences in the distribution of infected leaves between the background plot and the high SO_2 plot ($p < 0.01$). On 27 June there were differences between all treated plots and the background plot. On 15 June a fungicide was applied as a precaution against the further development of *S. tritici*, which was a serious risk in the surrounding areas (8). The application was not related to the presence of *E. graminis*. Mildew continued to increase in extent in SO_2-treated plots, with a few pustules observed on some fully emerged ears of plants exposed to 0.06 ppm SO_2.

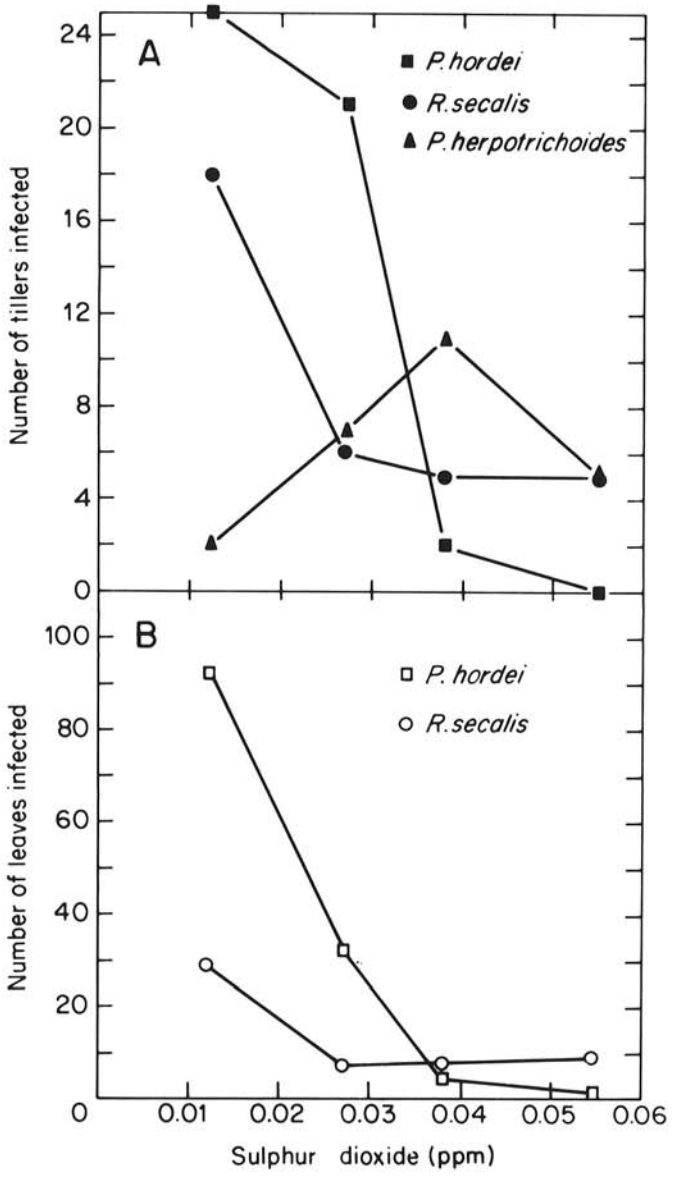

Fig. 1. A, The number of tillers of *Hordeum vulgare* in a random sample of 25 showing infection by *Puccinia hordei, Rhynchosporium secalis*, and *Pseudocercosporella herpotrichoides*. **B,** The number of the five youngest leaves of 25 tillers showing infection by *P. hordei* and *R. secalis* on 10 March 1983. SO_2 concentrations are the hourly mean exposure up to the date of observation.

Infection of tillers by *P. herpotrichoides* and *Fusarium* was assessed on 16 and 24 July (Fig. 3). In the medium SO_2 plot, the *P. herpotrichoides* infection decreased between 16 and 24 July, and this difference may be due to sampling error. A chi-square test revealed significant differences between plots in the proportion of tillers infected by *P. herpotrichoides* on 24 July ($p<0.001$) but not on 16 July. On 24 July the proportion of infected plants was significantly lower than the background plot in both the high and medium SO_2 plots ($p<0.001$).

On 16 July the proportion of tillers with *Fusarium* symptoms at both nodes was significantly different between plots ($p<0.01$), and all SO_2 plots had a lower level of infection that was significantly different from the background plot ($p<0.05$). Pink pustules were observed only in the control plot on 16 July but had developed in all plots by 24 July.

At the time of mildew development, the crop dry weight in the plot receiving the high SO_2 treatment was significantly lower than that in its controls (Table 4), and on 27 June measurements revealed a significantly higher leaf area index in the high SO_2 treatment plot than its controls (Table 4). This latter effect was visible as a greener circle within the ripening experimental field although mildew infestation was higher in this plot (Fig. 2). At final harvest there were no significant differences in crop dry weight between treated plots and their controls.

DISCUSSION

Evidence is presented indicating that exposure of cereal crops to elevated levels of SO_2 altered the development of certain fungal pathogens. The highest annual mean SO_2 concentration for a U.K. rural survey site during 1983–1984 was 0.026 ppm at Ratcliffe in central England (10), and the lowest treatment concentrations in these studies fall below this value. The highest annual mean of an urban survey site was 0.037 ppm measured at Doncaster in northern England (10), and this value is equalled or exceeded by the other treatments. The occurrence of fungi in the study is therefore relevant to ambient SO_2 exposures. Infestation of winter barley cultivar Sonja by brown rust (*P. hordei*) and leaf blotch (*R. secalis*) was reduced in plants exposed to 0.02, 0.04, and 0.06 ppm of SO_2 (Fig. 1 and Table 2). The exposed plants maintained a higher green leaf area index than the more heavily infected control plants and also achieved a higher crop dry weight before final harvest (Table 3). Conclusions at final harvest were complicated by the occurrence of BYDV throughout the experimental field, which reduced plant growth overall and increased variability in plant performance. The same barley crop showed a higher infestation with eyespot (*P. herpotrichoides*) at 0.04 ppm of SO_2 (Fig. 1). The mature wheat crop cultivar Rapier had a higher infestation of powdery mildew (*E. graminis*) at 0.02, 0.05, and 0.06 ppm of SO_2 (Fig. 2) and a lower infestation of eyespot (*P. herpotrichoides*) and brown foot rot (*Fusarium* spp.) (Fig. 3).

The interaction of plant pathogens and air pollution has been reviewed (19,26,27,40), and specific interactions have been investigated under controlled conditions (21,41). However, this is believed to be the first description of the natural occurrence of cereal pathogens during controlled open-air exposure of a crop to SO_2 throughout the growing season. The observations demonstrate the importance of air pollutant-pathogen interactions affecting crop growth under realistic field conditions. The direct effects of SO_2 alone may be the cause of the observed charges in crop growth, but it is likely that the reduced occurrence of rust in SO_2-treated plots also modified the growth of the exposed plants. Further experiments are required to test this possibility. There are additional economic implications since the unexposed plants crossed the disease threshold for recommended fungicide application (3), and the SO_2-exposed plants did not. This same consideration applies in reverse to the SO_2-mildew interaction, where crop growth appeared unaffected at final harvest, but the plants exposed to SO_2 crossed the disease threshold for fungicide treatment (3) and the unexposed control plants did not.

In open-air fumigation studies it is frequently difficult, for practical and economic reasons, to replicate expensive exposure systems, and there were no replicates of treatment plots in this study. Open-air release of gaseous pollutants may prevent the close proximity of plots exposed to different concentrations, while increasing the distance between plots can introduce problems of soil fertility gradients. In this study, two companion control plots were used to assist the interpretation of growth responses against any effects of background growth variation within the field. Without replication it is necessary to be cautious about conclusions drawn from individual experiments of this type. However, the observations reported are considered to represent real effects that are worthy of further investigation. As meteorological conditions and natural pathogen occurrence vary from year to year, repetition of the experiment will not necessarily produce similar results, but inoculation with test organisms of interest is a possible approach.

The mechanisms by which SO_2 may affect fungal pathogen occurrence include: direct effects on spore germination and fungal growth (26), changes in plant host suitability (42), changes in the phylloplane flora including competitive microorganisms (21), and changes in canopy structure that affect spore dispersal and

environmental conditions (38). It was not possible to exclude any of these effects as an explanation of the observations reported here. Except for periods when SO_2 exposure was terminated at wind velocities of less than 1 m s^{-1}, the fumigation continued when the vegetation was covered with dew or during rainfall. Although this may occur under natural conditions, deposition to the moisture on leaf surfaces during periods of high SO_2 concentration provides another possible mechanism for producing the observations reported. Further studies have revealed that the germination of *P. herpotrichoides* spores on distilled water agar was reduced by 46% by 24-hr exposure to 0.060 ppm SO_2 compared with controls exposed to 0.005 ppm of SO_2 in laboratory chambers (P. Mansfield, *unpublished data*). However, at the base of the plant canopy in the field, exposure to SO_2 is reduced by deposition to the leaves above. Measurements of SO_2 concentration at the base of a fumigated mature cereal canopy are frequently less than 10% of the concentration above the canopy (A. R. McLeod, *unpublished data*). Exposure of both mildew and eyespot infection sites to SO_2 was therefore considerably lower than the plant exposure. The different levels of rust infestation may also have affected the occurrence of eyespot by changing canopy density, possibly vertical SO_2 concentration profiles, and environmental conditions

TABLE 3. Total aboveground dry weight and leaf area index of a barley crop in plots fumigated with varying levels of SO_2 and in adjacent control plots during a natural occurrence of *Puccinia hordei*

		Total dry wt (g m^{-2})			Leaf area index		
Date	SO_2	Treatment	Controls[a]	% Change	Treatment	Controls[a]	% Change
6 January 1983							
	Background	125.8	122.2	3.0	0.88	0.82	7.3
	Low	141.8	126.0	12.5	0.88	0.78	12.1
	Medium	91.7	100.0	−8.3	0.69	0.69	0.1
	High	139.2	115.8	20.2	0.99	0.89	11.3
16 March 1983							
	Background	265.4	219.7	20.8	0.99	0.89	8.5
	Low	229.8	200.6	14.6	0.98	0.87	12.9
	Medium	195.5	179.1	9.2	1.22	0.72	68.7***[b]
	High	216.1	195.9	10.3	1.24	1.01	22.8*
27 April 1983							
	Background	408.5	370.6	10.2	1.44	1.40	2.9
	Low	411.1	332.8	23.5*	1.68	1.25	34.7***
	Medium	507.6	359.3	41.3***	2.44	1.59	53.6***
	High	489.8	413.6	18.4	2.50	1.63	52.7***
25 May 1983							
	Background	648.8	744.5	−12.9	1.65	1.91	−13.8
	Low	789.2	725.5	8.8	1.57	1.60	−2.1
	Medium	947.9	728.4	30.0***	2.18	2.11	3.4
	High	906.6	902.7	0.4	1.62	2.06	−21.3
5 July 1983							
	Background	1,045.8	993.5	5.2	...	...	...
	Low	1,208.2	1,013.7	19.2	...	...	...
	Medium	1,254.5	1,076.4	16.5	...	...	...
	High	1,111.3	1,182.9	−6.0	...	...	...

[a] Mean of two companion plots for each treatment plot.
[b] * and *** indicate differences significant at $P<0.05$ and $P<0.001$, respectively.

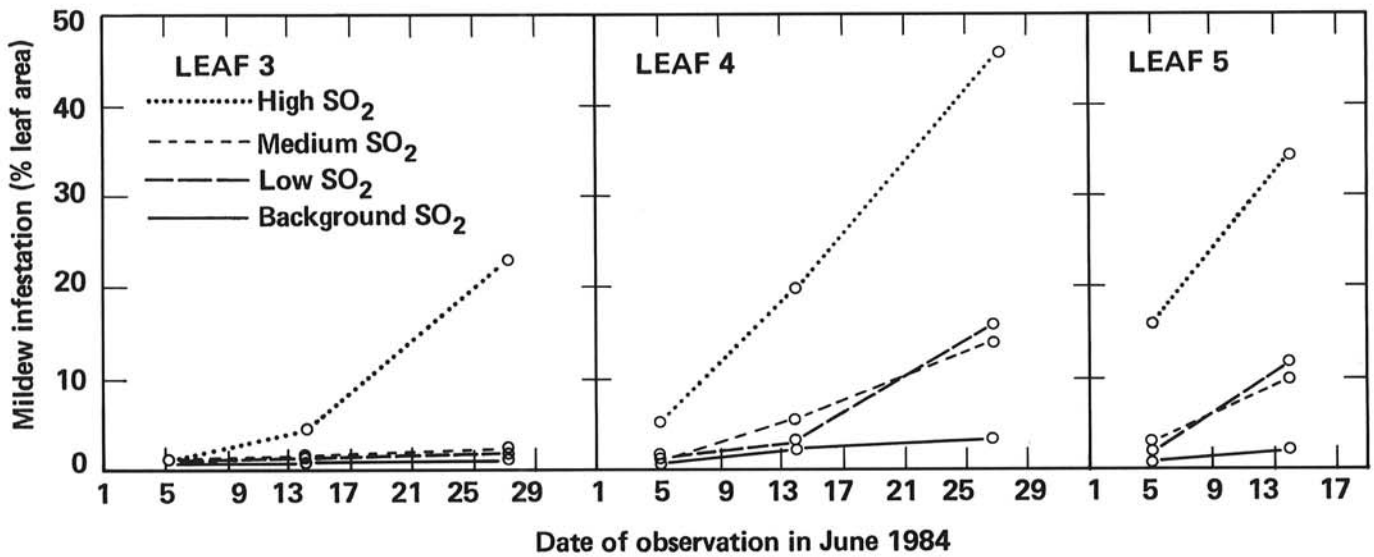

Fig. 2. The mean level of infestation of *Triticum aestivum* by *Erisyphe graminis* (measured as percent leaf area covered with pustules) at four SO_2 exposure concentrations and at each leaf position on three dates in June 1984. (Leaf number 1 [flag leaf] to leaf number 5 [oldest living leaf].)

(e.g., humidity). Changes in *P. herpotrichoides* infection resulting from humidity increases following leaf area increases have been reported (18). During the development of *E. graminis* on the wheat crop, field observations in July 1984 also detected increases in the numbers of grain aphid (*Sitobion avenae* (Fabricius)) with increasing SO_2 exposure (M. Aminu-Kano, *unpublished data*). Similar insect air pollutant interactions have been reported (15), and an increased input of honeydew to the lower leaves is yet another factor known to influence fungi growing on the leaf surface (16).

These results do not provide an explanation of the mechanisms of pathogen-air pollutant interactions, but they do demonstrate the possible complexity and importance of such interactions under field conditions. The majority of studies investigating the effects of air pollutants on crop growth are undertaken in open-top and closed chamber systems (23). Although chamber designs and operation may appear to provide a realistic physical environment for plant growth, the occurrence of pathogens (and insects) is rarely reported. *Botrytis* infection of onion has been reported but is reduced by the prevention of dew formation in chambers (42). During observations at this laboratory of cereal growth in closed chambers over 4 yr, the only pathogen observed was *E. graminis*. Moreover, in both open-top and closed chamber studies in the United Kingdom, the occurrence of *E. graminis* is often a problem and fungicide applications are necessary, at unrealistically frequent intervals (4–6 wk), to control the disease that otherwise severely restricts plant growth (T. M. Roberts, *personal communication*). Such fungicide applications are only rarely reported in the literature describing plant response to air pollutants (17,37).

Experiments under controlled chamber conditions are essential for determination of the direct effects of pollutants on vegetation. However, the absence of reports of pathogens (and insects) in many 'chamber' studies, the possibility of a modified response of pathogens in chambers, and the unrealistic use of fungicides raises questions about the validity of extrapolating results to the field where confounding factors such as fungal pathogens and insect pests may frequently modify the response. More research under field exposure conditions would be advantageous to assess the effects of SO_2 and other air pollutants on the occurrence of major crop diseases in different cultivars and under the variable meteorological conditions observed over several years.

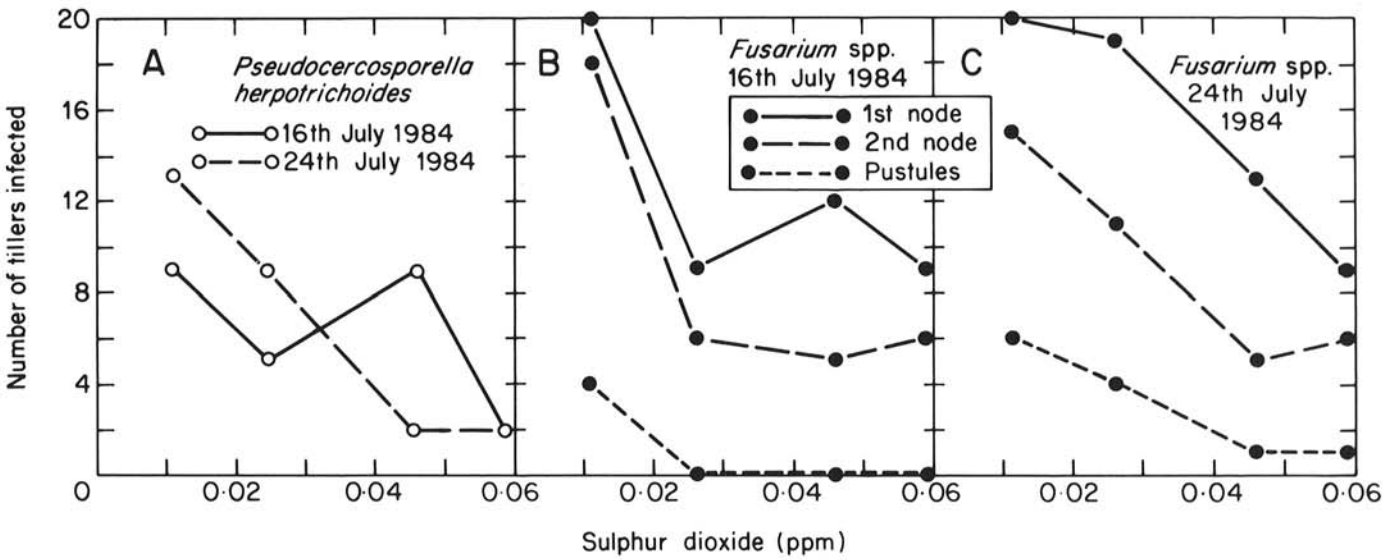

Fig. 3. The number of tillers of *Triticum aestivum* in a random sample of 25 showing infection by **A,** *Pseudocercosporella herpotrichoides* on 16 and 24 July 1984; **B,** *Fusarium* affecting the first (lowest) node, second node, and presence of pustules on 16 July 1984; and **C,** *Fusarium* on 24 July 1984.

TABLE 4. Total aboveground dry weight and leaf area index of a wheat crop fumigated with varying levels of SO_2 and in adjacent control plots during a natural occurrence of *Erysiphe graminis*

		Total dry wt (g m^{-2})			Leaf area index		
Date	SO_2	Treatment	Controls[a]	% Change	Treatment	Controls[a]	% Change
30 May 1984	Background	1,178.5	1,123.4	4.9	5.5	6.1	−9.5
	Low	1,124.2	1,171.3	−4.0	4.9	5.2	−5.2
	Medium	1,010.2	1,053.9	−4.1	4.5	4.1	8.6
	High	927.8	1,150.1	−19.3*[b]	4.9	4.4	10.7
27 June 1984							
	Background	1,870.8	1,875.3	−0.2	2.3	2.5	−7.9
	Low	1,742.9	1,783.9	−2.3	1.8	1.4	27.2
	Medium	1,669.7	1,862.2	−10.3	2.0	1.8	9.3
	High	1,638.2	1,867.9	−12.3	3.0	1.7	72.7***
8 August 1984	Background	2,380.0	2,316.8	2.7	...	...	...
	Low	2,142.7	2,256.6	−5.0	...	...	...
	Medium	2,258.2	2,088.0	8.1	...	...	...
	High	2,153.4	2,130.1	1.1	...	...	...

[a] Mean of two companion plots for each treatment plot.
[b] * and *** indicate differences significant at $P<0.05$ and $P<0.001$, respectively.

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