New Phytol. (1990), **115**, 357–365

The effects of long-term open-air fumigation with SO_2 on a field crop of broad bean (*Vicia faba* L.)

III. Quantitative analysis of damage components

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(*Received 4 September 1989; accepted 15 January 1990*)

SUMMARY

Effects of SO_2 on growth and production of broad bean, observed in three open-air fumigation experiments, were interpreted in terms of damage components with a mechanistic simulation model. The model consisted of an elementary model for crop growth, extended with submodels for the microclimate in the crop and with a submodel for uptake of SO_2 by leaves and for effects on leaf photosynthesis.

The major part of the observed reduction in total dry matter production could be explained by leaf injury observed in the oldest leaves of the fumigated plants at the end of the growing period. The effect consisted of dry matter loss through leaf abscission and a reduced growth rate at the end of the growth period due to reduction of the amount of absorbed radiation by the canopy. Direct effects of SO_2 on leaf photosynthesis explained an extra 10% of the observed yield loss (losses ranged from 7 to 17% of control yield). This small effect was confirmed by field measurements which showed no detectable effects of SO_2 on leaf and canopy photosynthesis. Increased leaf respiration, which was observed in the 1988 experiment, explained another 10% of the observed yield reduction.

Total SO_2-sulphur uptake by the fumigated crop, which is an important component of dry deposition of SO_2, was accurately simulated by the model.

Key words: *Vicia faba* L., sulphur dioxide, SO_2, air-pollution, open-air fumigation, yield, senescence, simulation model.

INTRODUCTION

Quantitative assessment of the effects of air pollutants, especially SO_2, on crop yield has been a major issue of research on air pollutant effects on ecosystems. The extensive published data on crop loss in fumigation experiments have been compiled and summarized with simple descriptive dose–response models for effects of SO_2 on grasses (Roberts, 1984) and dicotyledonous crops (McLaughlin & Taylor, 1985). They noted a considerable variability in responses to SO_2 between different species, between years within the same species and between different exposure systems, ranging from laboratory growth chambers to open-air exposure systems. Results obtained by controlled laboratory or greenhouse studies, representing a very broad range of species and exposure conditions, provided no indication of a consistent relationship between pollutant dose and plant response (McLaughlin & Taylor, 1985).

Accurate prediction of SO_2 effects on crop production in field situations with descriptive dose-response relationships fitted to experimental data is very difficult because plant responses to SO_2 are strongly influenced by environmental factors (e.g. windspeed, radiation, temperature) and by the physiological status of the plant (Black, 1982).

In descriptive empirical models like dose-response relationships, the mechanisms by which the crop responds to its environment are considered to be a black box. Since the variation in plant responses to SO_2 is likely to be related to metabolic mechanisms, more accurate predictions of the impact of air pollutants on crops should be based upon understanding of the effects of air pollutants on physio-

logical processes which determine crop growth and production. Such knowledge can be incorporated into existing deterministic models for crop growth and production which have been developed in the past few decades (de Wit *et al.*, 1978; Penning de Vries & van Laar, 1982). These models have been successfully applied to growth and production of forest stands (Mohren, 1987). Models for the effects of SO_2 on crop growth and production should simulate the uptake of SO_2 by the canopy, the metabolism of SO_2 and the effect of its metabolites on physiological processes. Such deterministic models may help to identify the complex relations between plant growth and effects of air pollutants at the metabolic level.

Much experimental work has been conducted on the analysis of air pollutant effects, and in particular SO_2, on crops and vegetation at various levels of resolution ranging from the biochemical to the ecosystem level (cf. Ziegler, 1975; Hållgren, 1978; Unsworth & Ormrod, 1982). However, relatively few attempts have been made to integrate this extensive amount of information into mechanistic models, and to interpret the various observed phenomena (Kercher & King, 1985; Krupa & Kickert, 1987).

The aim of the present study was to interpret the effects of SO_2 on crop yield with a mechanistic model, and to quantify the contributions of different physiological effects to the loss in crop yield which have been observed in three field experiments with broad bean exposed to SO_2 in the field (Kropff *et al.*, 1989*a*, *b*). In 3 years, the crops were exposed to mean concentrations of 165 μg SO_2 m^{-3} (in 1985), 62 μg SO_2 m^{-3} (in 1986) and 74 μg SO_2 m^{-3} (in 1988). In all years no effects on plant growth were found during the vegetative phase. A final reduction in total dry matter of 17% was observed in 1985 and 9% in 1988. In 1986, a severe infection of the control crop with the fungal pathogen *Botrytis fabae* occurred in the pod filling period. Slight *B. fabae* infections were also observed in the control plots in 1985 and 1988. Reduction of plant growth was accompanied by a strong reduction in leaf area at the end of the growing season. This was mainly due to damage in the older leaves, which first showed red-brown coloured necrotic spots, starting at the margins of the leaf. The symptoms clearly differed from the symptoms which may be observed as a result of known disease infections (Gerlach, personal communication). To enable the quantification of the contributions of different physiological effects to the observed loss in crop yield, a crop growth model was extended with submodels for the microclimate in the crop canopy, and a submodel for the uptake of SO_2 by leaves and subsequent effects of SO_2 on leaf physiology (Kropff, 1989*a*, *b*; Kropff & Goudriaan, 1989).

MATERIALS AND METHODS

Experimental design

In 1985, 1986 and 1988, the effect of an elevated SO_2 concentration on field crops of broad bean (*Vicia faba* L.) was studied by using a computer-controlled open-air exposure system (Mooi & van der Zalm, 1986), which consisted of a circular network of stainless steel piping with a diameter of 30 m. SO_2 was released from the upwind section exposing broad bean to 165 μg SO_2 m^{-3} in 1985, 62 μg SO_2 m^{-3} in 1986 and 74 μg SO_2 m^{-3} in 1988 (seasonal means). The control plot was located 250 m from the system. The ambient background concentrations were 16 μg SO_2 m^{-3} in 1985, 7 μg SO_2 m^{-3} in 1986 and 9 μg SO_2 m^{-3} in 1988. Details on the spatial and temporal distributions of the SO_2 gas in the system, weather conditions and O_3 concentrations are given by Kropff *et al.*, 1989*a*. The plants were grown in plastic containers (55 × 22 cm, with a height of 25 cm) filled with a commercial potting mixture. Water was supplied with a drip irrigation system.

Plant growth was analysed by frequent harvesting. In 1986, the experiment was terminated following a severe *Botrytis* infection in the control plants. Total sulphur was analysed in the different organs with a Carbo Erba Elemental Analyser. Further experimental details are given by Kropff *et al.* (1989*a*).

Measurement of photosynthesis and respiration

Long-term effects of SO_2 exposure on leaf photosynthesis were measured in 1985, 1986 and 1987 (in 1987 an extra experiment was conducted to study the effects of SO_2 on photosynthesis during 8 days after the onset of the exposure) with portable equipment consisting of a leaf chamber, an air supply unit and a portable CO_2 analyser (Analytical Development Co. Ltd, Herts, England). Photosynthesis of the youngest fully unfolded leaf was measured 79 days after crop emergence in 1985, while in 1986 photosynthesis in 2 leaves (leaf numbers 10 and 15, from the bottom of the canopy) was measured 63 and 78 days after emergence. In 1987, plants with about 10 leaves were placed in the open-air fumigation experiment to measure the medium-term effects of SO_2 on leaf photosynthesis. Photosynthesis of the fifth leaf was measured by repeated measurements in the field over a period of 8 days at high radiation levels.

Dark respiration (determined on 5 different numbered leaves) was measured in 1988 around the onset of the pod filling period, when the first leaf injury symptoms had been observed. Dark respiration was measured according to de Visser (personal communication), using Warburg equipment for the analysis of O_2 consumption of leaf discs (Umbreit, Burris & Stauffer, 1957). Dark respiration was measured 3 h after incubation.

Canopy photosynthesis of control and fumigated plants was measured around the onset of pod filling in 1988 with a mobile system described by Louwerse & Eikhoudt (1975) and Louwerse (1980). Two containers, with seven plants were placed in each of two enclosure chambers (80 × 80 × 80 cm) consisting of transparent acrylic, sealed onto a metal frame. The air flow containing ambient CO_2 concentration (340 ppm) through the whole system was about 0·03 m^3 s^{-1}, which corresponds with a residence time of about 20 s (volume = 0·6 m^3). The enclosure system operates as an open system with overpressure to avoid effects of leakage and soil respiration. Photosynthesis was measured under natural radiation in four replicates. The temperature in the chambers was 20 °C during the day and 14 °C at night. Global radiation was measured with a Kipp solarimeter near the chambers. SO_2 was injected into the air inlet of the chambers with a mass flow controller, which was adjusted manually. Air from the chambers was sampled through teflon tubing, and SO_2 concentrations were analysed with a fluorescent SO_2 analyser, Monitor Labs (model 8850).

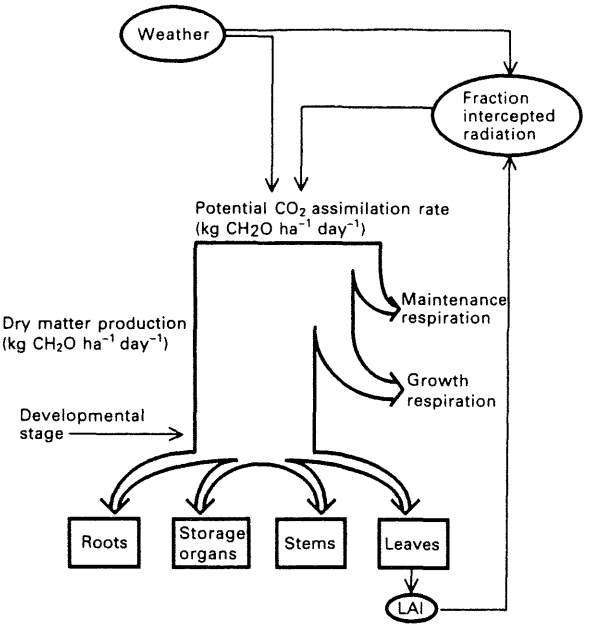

Figure 1. A schematic representation of the simulation model for crop growth. Boxes represent amounts and arrows indicate flows of material. Lines indicate flows of information.

MODEL DESCRIPTION

General structure of the model

The model simulates the effects of SO_2 on crop growth in potential production situations where growth is only determined by the incoming radiation, temperature and some physiological characteristics of the species. Water, nitrogen and other nutrients are assumed to be abundant and the crop is assumed to be free of pests, diseases and weeds. The model consisted of an elementary model for crop growth (Spitters, van Keulen & van Kraalingen, 1989; de Wit *et al.*, 1978; Penning de Vries & van Laar, 1982), a submodel for the microclimate inside the canopy and a leaf submodel for the uptake of SO_2 by the leaf, the metabolism of S(IV) ($S(IV) = [SO_2]_{aq} + [HSO_3^-] + [SO_3^{2-}]$) in the leaf and effects on stomatal conductance and photosynthesis (Kropff, 1987, 1989*a*, *b*; Kropff & Goudriaan, 1989). The model operates with time steps of one day, but allows for daily variation in radiation. Figure 1 gives a schematic representation of the elementary model for crop growth, the core of which is formed by the calculation of canopy photosynthesis and respiration on the basis of processes at the organ level. The daily dry matter production is distributed over the various plant organs dependent on the developmental stage. Numerical integration in time gives the time-course of dry matter. The inputs required by the model are listed in Table 1.

Simulation of canopy photosynthesis

Daily gross canopy photosynthesis was calculated from daily total global radiation, daily maximum and minimum temperature and the leaf area index (LAI) of the crop, following the procedure given by Goudriaan (1982, 1986), Spitters (1986) and Spitters, Toussaint & Goudriaan (1986).

Daily photosynthesis was calculated from an assumed diurnal weather pattern based on daily totals of radiation or means of temperature and windspeed (Spitters *et al.*, 1986). The rate of photosynthesis was calculated each hour from the absorbed photosynthetically active radiation and the light response of photosynthesis in individual leaves. The hourly values of canopy photosynthesis were obtained by using the Gaussian integration technique for integration of photosynthesis over the LAI of the canopy (Goudriaan, 1986).

Table 1. *Experiment-specific model inputs*

1. Daily maximum and minimum temperature	°C
2. Daily total global radiation	MJ m^{-2} d^{-1}
3. Date of emergence and final harvest	Day of the year
4. Hourly values of SO_2 concentration	μg m^{-3}
5. Measured Leaf Area Index as a function of time	m^2 m^{-2}

From the windspeed above the canopy, the turbulent resistance of the canopy and the boundary layer resistance of the leaves in the canopy were calculated as a function of height according to Goudriaan (1977). Stomatal conductance of leaves at a certain height in the canopy was calculated from the rate of leaf photosynthesis (determined by the amount of absorbed radiation) and the boundary layer resistance at that height in the canopy. Uptake of SO_2 and effects on leaf photosynthesis were calculated according to the stationary state version of the leaf submodel, described by Kropff & Goudriaan (1989).

Simulation of dry matter growth

The growth rate of the crop canopy (dY/dt, dry matter in kg ha^{-1} d^{-1}) was then calculated according to:

$$\frac{dY}{dt} = (A - R_m)/G,$$

where A denotes the gross rate of canopy photosynthesis (kg CH_2O ha^{-1} d^{-1}), R_m the maintenance respiration (kg CH_2O ha^{-1} d^{-1}), and G the glucose requirement for the formation of structural dry matter from sugars (kg CH_2O kg^{-1} dry matter). The dry matter produced was distributed over the organs depending on the developmental stage. Phenological development was linearly scaled from emergence to the onset of pod filling, and from the onset of pod filling to maturity. At stage 0 the crop emerged, at stage 1 pod filling started and maturity was reached at stage 2. The developmental rate was calculated as a function of daily mean temperature. Further details are given by Spitters *et al.* (1989).

Parameterization

The parameters for the photosynthesis light response curve and their dependence on temperature and development stage were derived from Grashoff, Klein Hulze & Smid (1987), and from our own data. Standard values for maintenance respiration coefficients were used (Spitters *et al.*, 1989). Allowance was made for the decrease of these coefficients with plant development by relating them to the nitrogen content of the stems and leaves. The relation between developmental rate and temperature was derived from Grashoff *et al.* (1987). The dry matter distribution functions for above-ground organs in the model were based on the first two field experiments (Kropff *et al.*, 1989*a*, *b*). The dry matter distribution pattern in the 1988 experiment clearly differed from the other two experiments for both the control and the fumigated crop. In 1988, the pod filling period started at a later calculated developmental stage than in 1985 and 1986. A slight water stress at the onset of pod filling may have favourable effects on pod production, and especially on early pod growth (Grashoff *et al.*, 1987). It is likely that such a slight water stress occurred around the beginning of the pod filling period in 1985 and 1986, because the capacity of the drip irrigation system was lower in 1985 and 1986 than in 1988 since in the 1988 experiment less plants were grown.

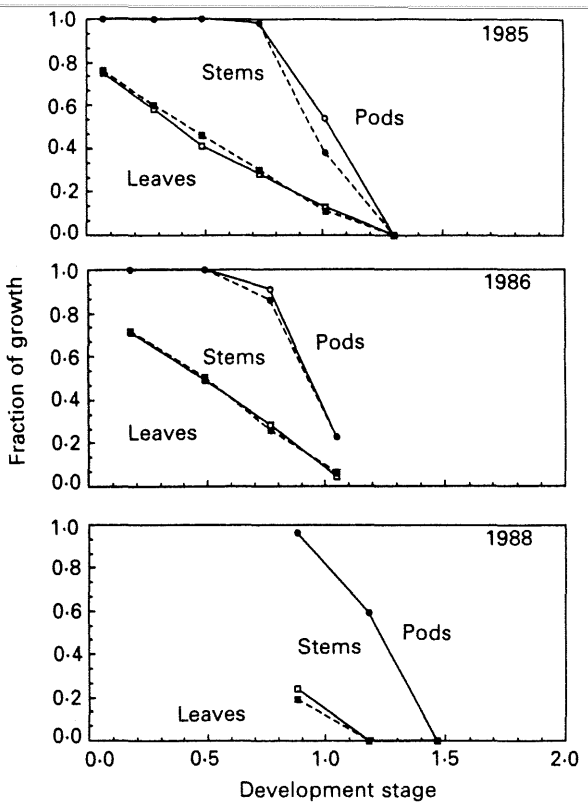

Figure 2. Dry matter distribution over the plant organs of *Vicia faba* L. as a function of developmental stage (0, emergence; 1, onset of pod filling; 2, maturity), for control (open symbols and solid lines) and fumigated plants (closed symbols and dashed lines) in 1985, 1986 and 1988.

The fractions of dry matter allocated to the different above-ground plant organs were not affected by SO_2 in any of the experiments (Fig. 2), and consequently effects of SO_2 on the distribution pattern of dry matter were not included in the model. Since root growth was not determined in the experiments, no account could be taken of effects on dry matter distribution between shoot and root. The relative death rate of the leaves (d^{-1}) in relation to developmental stage and exposure regime was estimated for the control and the fumigated crops in all experiments. Experiment-specific relative death rates were used in the model, because SO_2 strongly influenced the relative death rate of the leaves.

Procedure of quantitative interpretation of SO_2 effects observed in the field experiments

Model performance was first evaluated by comparing its results with the three experimental data sets on

the growth of broad bean in the control plots, with one set of parameters and functions describing species characteristics. Since the model was used for a quantitative explanation of the background of effects of SO_2 on crop growth rates, the LAI was not simulated in the model, but the measured LAI was used in the model. This enables the separation of SO_2 effects on crop growth occurring as a result of a reduced light interception caused by leaf necrosis, from direct effects of SO_2-derived metabolites on physiological processes.

The observed effect on green leaf area was first introduced in the model to analyse the contribution of only the reduction of LAI to the observed yield loss. The leaf submodel for SO_2 effects on photosynthesis was then introduced followed by the analysis of the effect of increased leaf maintenance respiration with the model.

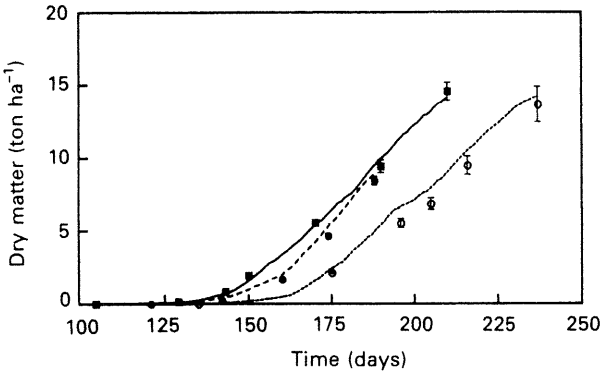

Figure 3. Observed and simulated total dry matter production of the control crops in 1985 (■, observed; ——, simulated); 1986 (●, observed; – – –, simulated) and 1988 (○, observed; ····· simulated).

RESULTS AND DISCUSSION

Simulation of control crops

Observed and simulated production of total above-ground dry matter of control crops are presented in Figure 3. Growth and production of the broad bean crops was accurately simulated for all experiments with the set of parameters for species characteristics.

Yield reduction due to leaf injury in fumigated crops

Leaf injury was observed in the fumigated plots in each experiment, resulting in strong reductions of LAI at the end of the growing period (Kropff *et al.*, 1989*b*). As leaf injury proceeded from older to younger leaves, it was unnecessary to account for shading of green leaves by yellow or dead leaves in the model. Introduction of the measured (green) LAI of fumigated crops explained much of the reduction in total dry matter in all three experiments: 69 % in 1985, 69 % in 1986 and 86 % in 1988 (Table 2, simulation expt 1). The effect of reduced leaf area in fumigated crops, resulting in reduced absorbed radiation, was largely responsible for this effect in 1985 and 1988 (Table 2). The reduction of the seasonal amount of absorbed radiation was 7·2 % in 1985, 3·8 % in 1986 and 4 % in 1988. The simulated effect of the damage components on pod production is given in Table 3 for the experiments in 1985 and 1988. These results yield the same picture as those from the analysis of reductions in total dry weight. The 1986 experiment was omitted, since the crops were not harvested because of a severe *Botrytis* infection in the control plots (Kropff *et al.*, 1989*a*).

The time-course of difference in total dry matter between control and exposed plants was simulated accurately until the final harvest, by only taking into account the differences in leaf area development between the treatments (Fig. 4). This illustrates that leaf injury at the end of the growing period was largely responsible for the reductions in total above-ground dry matter.

Table 2. *Damage components of reduction in total dry matter kg ha^{-1}, at final harvest in three field experiments with* Vicia faba *exposed to ambient or elevated SO_2 concentrations in 1985 (165 $\mu g\ m^{-3}$), 1986 (62 $\mu g\ m^{-3}$) and 1988 (74 $\mu g\ m^{-3}$)*

	Dry matter (kg ha^{-1})		
Experiment	1985	1986	1988
Observed control yield	14534	8454	13661
Observed reduction	2528	630	1240
Simulated reduction caused by individual components			
(1) Effects on leaf area development			
Leaf abscission	479	229	426
Reduced light interception	1256	210	641
(2) Direct effects on photosynthesis	212	70	92
(3) Effects on leaf respiration	202	145	201
(1)+(2)+(3)	2149	654	1360

Table 3. *Damage components of yield reduction in kg dry matter (pods) ha^{-1}, at final harvest in two field experiments with* Vicia faba *exposed to ambient or elevated SO_2 concentrations in 1985 (165 μg m^{-3}) and 1988 (74 μg m^{-3})*

	Dry matter (kg ha^{-1})	
Experiment	1985	1988
Observed control yield	7888	7707
Observed yield reduction	1780	787
Simulated yield reduction caused by individual components		
(1) Effects on leaf area development	841	719
(2) Direct effects on photosynthesis	116	69
(3) Effects on leaf respiration	126	140
(1)+(2)+(3)	1083	928

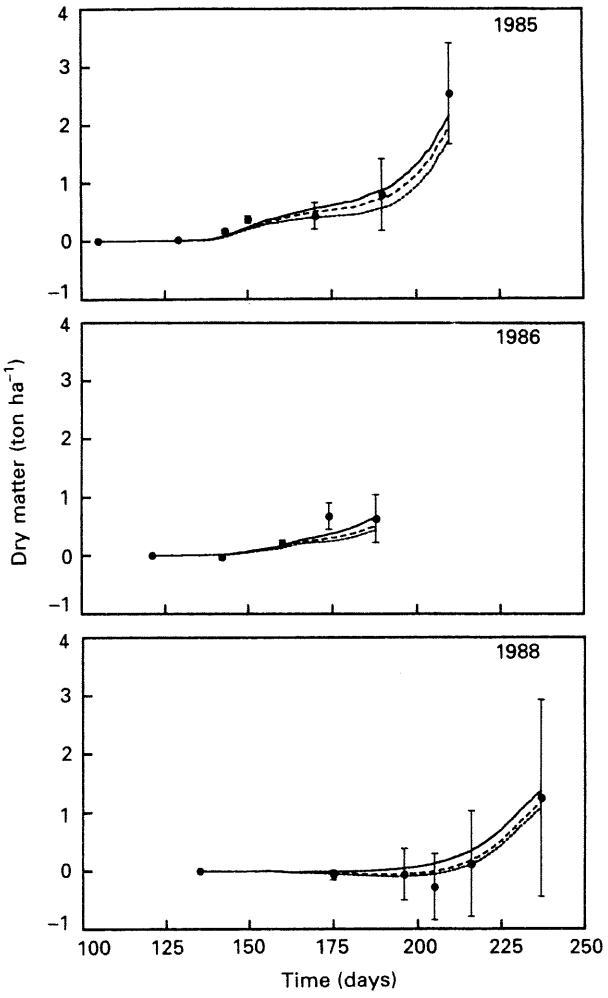

Figure 4. Observed (•) and simulated difference in total dry matter production between the control and fumigated crop in 1985, 1986 and 1988. Three damage components were evaluated: (1) effect of differences in leaf area development and leaf fall (·····); (2) effect of (1) with an additional effect of SO_2 on photosynthesis (– – –), and (3) effect of (2) and an elevated maintenance respiration of the leaves (——).

The effect of reduced photosynthesis

Introduction of the submodel for uptake and effects of SO_2 on photosynthesis slightly improved the simulation results. An additional amount of the reduction (0·7–1·5 %) in total dry matter production was explained from direct effects of SO_2 on photosynthesis (Table 2), namely 10 % in 1985, 11 % in 1986 and 6 % in 1988. Comparable effects on pod production were simulated (Table 3). The effect of SO_2 on photosynthesis of leaf canopies at the concentrations applied here was small as was expected on basis of the findings reported by Kropff & Goudriaan (1989).

The submodel for SO_2 effects on leaf photosynthesis is based on observations from short-term fumigation experiments. The role of additional long-term effects on photosynthesis at the concentrations which were applied in the field (100/200 μg m^{-3}), was analysed by field measurements of leaf and canopy photosynthesis. These measurements were conducted in 1985, 1987 and 1988. In 1985, no effects on photosynthesis at light saturation were detected after a long exposure period (Table 4). Measurements of photosynthesis on the 5th leaf at high radiation levels during an 8-day fumigation period in 1987, also showed no long-term effects on photosynthesis (Table 5). Measurements on photosynthetic efficiency of whole canopies showed no difference between control and fumigated crops. Between 10 and 100 J m^{-2} s^{-1} (PAR, photosynthetically active radiation, absorbed by closed canopies with an LAI > 6), the photosynthetic efficiency of the control crop was 12·3 g CO_2 MJ^{-1} (SE 0·7) and of the fumigated crop 12·0 g CO_2 MJ^{-1} (SE 0·5).

The effect of increased respiration

Dark respiration of leaves was measured in 1988 around the pod filling period. Although quantitative

Table 4. *Net rate of CO_2 assimilation ($\mu g\ CO_2\ cm^{-2}\ h^{-1}$) of leaves of broad bean exposed to ambient or elevated SO_2 concentrations in 1985 (165 $\mu g\ SO_2\ m^{-3}$), of leaf numbers 10–14, 79 days after emergence. Radiation in $J\ m^{-2}\ s^{-1}$ (PAR) (n = 14)*

Control		Fumigated	
Photosynthesis ($\mu g\ CO_2\ cm^{-2}\ h^{-1}$)	Radiation ($J\ m^{-2}\ s^{-1}$)	Photosynthesis ($\mu g\ CO_2\ cm^{-2}\ h^{-1}$)	Radiation ($J\ m^{-2}\ s^{-1}$)
303	305	265	326

Where analysis of variance showed a significant difference between the treated plants and the control plants, the treated plants means are indicated as: $*P < 0.05$; $**P < 0.01$; $***P < 0.001$

Table 5. *Net photosynthesis ($\mu g\ CO_2\ cm^{-2}\ h^{-1}$) of the fifth leaf number of* Vicia faba *exposed to ambient or elevated SO_2 concentrations in 1987 (100 $\mu g\ SO_2\ m^{-3}$), in relation to the number of days after the start of fumigation. Plants had about 10 leaf layers*

		Control		Fumigated	
Days	*n*	Photosynthesis ($\mu g\ CO_2\ cm^{-2}\ h^{-1}$)	Radiation ($J\ m^{-2}\ s^{-1}$)	Photosynthesis ($\mu g\ CO_2\ cm^{-2}\ h^{-1}$)	Radiation ($J\ m^{-2}\ s^{-1}$)
0	20	255·6	232·6	259·5	239·7
2	6	276·7	202·0	284·4	208·1
7	16	237·6	246·1	231·8	247·1
8	4	269·2	267·3	254·7	223·2

Where analysis of variance showed a significant difference between the treated plants and the control plants, the treated plant means are indicated as: $*P < 0.05$; $**P < 0.01$; $***P < 0.001$

interpretation of dark respiration of leaf discs in terms of maintenance respiration is speculative, relative differences between treatments or varieties appeared to be consistent (de Visser, personal communication). A significant ($P < 0.001$) increase of respiration (*c.* 30%) in fumigated leaves was observed, which appeared to be independent of leaf age (characterized by leaf number) (Fig. 5). Similar results were obtained in 1985 when plants were transported from the field and photosynthesis of the youngest fully unfolded leaf was measured over a period of two days. The above findings may be interpreted as an increased rate of leaf maintenance respiration, since the leaves were fully grown. It seems reasonable to assume that the effect on respiration is independent of the length of the fumigation period, since all leaf layers showed the same pattern.

Introduction of an increased rate of maintenance respiration of the leaves throughout the growing season slightly improved the simulation of the depression of dry matter and pod production. The time course of observed and simulated yield loss (Fig. 4), however, indicates that an additional effect at the end of the growing season, rather than an increased maintenance respiration throughout the growing season, must have played a role. No consistent effects of SO_2 on respiration have been reported: both stimulating and inhibitory effects have been observed (cf. Black, 1984). More research on the interpretation of dark respiration in terms of maintenance respiration and effects of air pollutants is necessary.

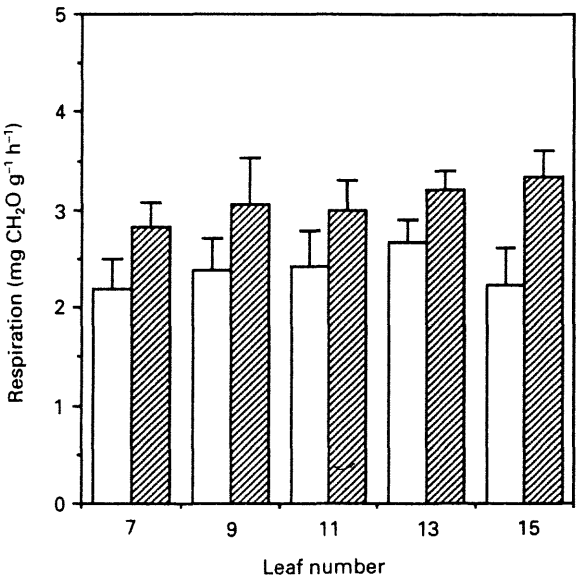

Figure 5. Rates of dark respiration measured 3 h after incubation for five leaf numbers of control (□) and fumigated (▨) plants from the 1988 experiment at the onset of the pod filling period.

Damage components

The analysis indicated that most of the observed reduction in total dry matter production can be explained by observed effects on leaf area development of the exposed plants, i.e. leaf fall and a reduced growth rate at the end of the growing season. Including direct effects of SO_2 on photosynthesis and leaf respiration improved the simulation results slightly. Leaf injury occurred on the older leaves after long-term exposures to low SO_2 concentrations in our experiments and was also observed by Guderian (1977) and Pierre & Queiroz (1981, 1982). However, Baker *et al.* (1986), Baker, Fullwood & Colls (1987) and McLeod *et al.* (1988) did not observe chronic leaf injury, but often a stimulation of leaf area development in summer in their field experiments with barley exposed to SO_2. McLeod *et al.* (1988) even reported a delay in leaf senescence in the fumigated plots. This leads to the conclusion that prediction of the effect of continuous exposure of crops and forests to low SO_2 concentrations with mechanistic models requires quantitative insight in the physiological mechanisms of chronic leaf injury.

Simulation of SO_2 uptake by the canopy

The average deposition velocity (calculated from the rate of extra S uptake by the fumigated crop and the average concentration of SO_2) was about 5 mm s^{-1}, which is close to measured values of 8 mm s^{-1} in the daytime and 4 mm s^{-1} during the night for a wheat crop of which 3·5 mm s^{-1} was caused by deposition to leaf surfaces and soil (Unsworth *et al.*, 1985). The measured and simulated uptake of total sulphur by the canopy in 1985 and 1988 (total sulphur was not measured in 1986) are presented in Figure 6. The observed sulphur uptake is defined here as the difference in sulphur content between the fumigated and control crop. The uptake of S by the 1985 crop was accurately simulated with the model, but the uptake of total S in 1988 was somewhat underestimated. The simulated underestimation of S uptake for the 1988 experiment may have been caused by the higher humidity in 1988 (80·4 °$_0$ in 1988 and 74·7 °$_0$ in 1985), because a strong relationship exists between VPD (vapour pressure deficit) in the air and the ratio of the internal CO_2 concentration (C_i) and the ambient CO_2 concentration (C_a) (Morison, 1987). Simulated S uptake appears to be extremely sensitive to the ratio between internal and external CO_2 concentration. The amount of S taken up by the fumigated crop in 1988 changed from 14·0 kg S ha^{-1} to 17·76 kg ha^{-1} when the ratio C_i/C_a was changed from 0·8 to 0·85. This illustrates that more insight in stomatal behaviour in relation to environmental conditions is needed for calculation of air pollutant uptake. Canopy transpiration is less sensitive to stomatal conductance because of the interrelationship between transpiration, leaf temperature and the difference in vapour pressure between the leaf and the air.

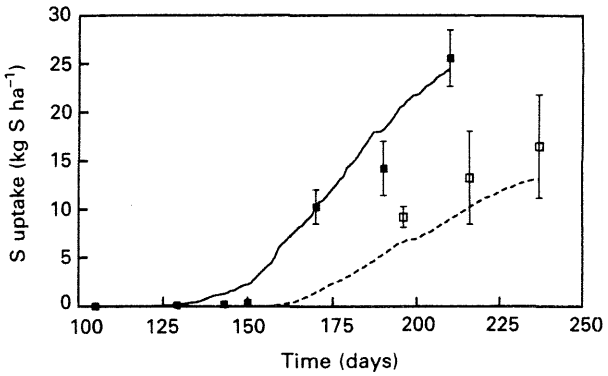

Figure 6. Observed and simulated extra S uptake by the fumigated crop in 1985 (■, observed; ——, simulated) and 1988 (□, observed; – – –, simulated).

ACKNOWLEDGEMENTS

This work was supported by the Dutch Priority Programme on Acidification. I am very grateful to W. Smeets, A. J. A. van der Zalm, G. Lahey, F. de Koning, P. Pasmans, H. Peppelenbos, E. de Ruiter, A. Kooyman, I. van Veelen and I. Eldeleklioplu for their contributions to the experiments. I thank N. C. van Keulen for conducting chemical analyses, M. J. de Kock and R. de Visser for determining respiration rates of leaves and J. van Kleef, W. Louwerse for measuring photosynthesis of enclosed canopies. C. T. de Wit, J. Goudriaan, M. H. Unsworth, E. A. Adema, H. H. van Laar and D. W. G. van Kraalingen are acknowledged for stimulating discussions and comments on the manuscript.

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