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Modelling short-term effects of sulphur dioxide.
3. Effects of SO_2 on photosynthesis of leaf canopies

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Abstract

The effect of short-term exposure of SO_2 on the photosynthesis of a Faba bean crop was analysed with mobile equipment in the field. Canopy photosynthesis was only affected at high radiation levels and reduced by 4-6% during fumigation with 800 μg SO_2 m^{-3}.

The experimental data were used to evaluate the performance of a model for the effects of SO_2 on leaf canopy photosynthesis. The model contained a calculation procedure for canopy photosynthesis, extended with a submodel for SO_2 uptake by leaves and effects of SO_2 on leaf physiology. Diurnal photosynthesis and the effect of SO_2 on canopy photosynthesis were approximated very closely with the model. Possibilities for the application of this approach in crop growth models (operating at a time step of integration of 1 day) are presented and evaluated.

Additional keywords: simulation model, sulphur metabolism, pollution.

Introduction

The effect of SO_2 on photosynthesis of leaves and whole plants has been studied extensively in order to find a mechanistic explanation for growth reductions in plants exposed to SO_2 in the absence of visible injury. Most workers observed depressing effects of SO_2 on leaf or plant photosynthesis (Bennet and Hill, 1973; Black, 1982; Black and Unsworth, 1979a, b; Darrall, 1986; Kropff, 1987). The general pattern of photosynthetic reduction after the onset of fumigation is a rapid decline in photosynthesis, followed by stabilization within 30-120 minutes (Kropff, 1987). A model was described earlier (Kropff, 1989a) to simulate SO_2 uptake, the balance of toxic metabolites in the leaf and effects of toxic S(IV) compounds on rates of photosynthesis. To simulate leaf photosynthesis during fumigation with SO_2, two parameters to be quantified are the time coefficient for S(IV) oxidation and the parameter which describes the sensitivity of photosynthesis with respect to the S(IV) concentration. Values for these two key parameters are relatively easy to obtain from data on photosynthesis during a fumigation period and a subsequent period of recovery (Kropff, 1989b). The model provides a good description of the behaviour of leaf photosynthesis during short-term SO_2 exposure periods (Kropff, 1989a, b).

To evaluate the impact of atmospheric pollutants on crops and vegetation, models for the effect of air pollutants on leaf physiology can be incorporated into models for growth and production of crops and vegetation. Such combination models enable the estimation of effects without doing expensive, and in the case of forests almost impossible, experiments. However, realistic prediction demands that such models be based upon thorough insight in the effects of air pollutants on crop physiology. The effects of SO_2 on photosynthesis of leaf canopies based on observations on single plants, was first modelled by Black and Unsworth (1979a). They predicted 65% reduction in daily total net photosynthesis of a *Vicia faba* canopy with a leaf area index of 4 when exposed to 95 $\mu g\ SO_2\ m^{-3}$. This is not likely to be a realistic prediction for field crops, since only small yield reductions have been observed when crops were exposed to low SO_2 concentrations in the field. In 1985, we exposed field crops of *Vicia faba* to elevated SO_2 concentrations (100-200 $\mu g\ SO_2\ m^{-3}$) and analysed growth and production. Crop growth was reduced by 17% at the end of the growing season, but effects on the growth rate were only observed at the end of the growing season, in the pod filling period (Kropff et al., 1989). No effects could be detected in the linear growth phase. In other field studies with barley, no clear effects on total dry matter growth and only small yield reductions were observed at low SO_2 concentrations ($<$ 150 $\mu g\ SO_2\ m^{-3}$ as a seasonal average) (Baker et al., 1986; McLeod et al., 1988). This illustrates the importance of validation of models used to predict air pollutant effects on leaf canopies based on observations on laboratory grown plants.

The aim of this study was to experimentally analyse the short-term effects of SO_2 on photosynthesis and transpiration on a Faba bean crop and to evaluate the performance of a model for the effects of SO_2 on photosynthesis of leaf canopies by comparing simulation results with experimental data.

Materials and methods

Equipment for measurement of photosynthesis of leaf canopies. Measurement of photosynthesis and transpiration of enclosed canopies were performed with a mobile system, described by Louwerse and Eikhoudt (1975) and Louwerse (1980). Data logging and processing was performed by a PDP11 minicomputer. The enclosure chamber (80×80×80 cm) consisted of transparent acrylic, sealed on a metal container (80×80×65 cm) in which the plants were grown. The measurement system was placed outdoors to obtain a natural time course of radiation. 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 seconds (volume = 0.6 m^3). The enclosure system operates as an open system with overpressure to avoid effects of leakage and of soil respiration.

Total global radiation was measured with a Kipp solarimeter, air temperature with copper/constantan thermocouples and air humidity with Vaisala probes. SO_2 was bled into the air inlet (unfiltered air) of the chambers regulated via mass flow controllers from a cylinder (2000 ppm SO_2 in N_2). Since the flow of circulating air in the chamber was 10 times as high as the net replacement flow, SO_2 was well mixed. SO_2 concentration in the chambers was measured with a fluorescent SO_2 analyser (Monitor Labs, model 8850). Air was conducted from the chambers through teflon tubing by a teflonized pump. The incoming SO_2 flow was continuously adjusted manually to prevent large changes in SO_2 concentration in the chambers. The air temperature was maintained at 20 °C during the photoperiod and at 15 °C during the night.

Plant material. *Vicia faba* (cv. Minica) was sown in the glasshouse in pots filled with a commercial potting soil in the beginning of April 1988. One week before the measurements started, the plants were placed in metal containers and placed outdoors under a transparent roof to prevent frost damage.

Measurement procedure. Net photosynthesis of 2 enclosed canopies was measured simultaneously between 18-27 April 1988, at the Centre for Agrobiological Research in Wageningen. After one week of measurement new containers with plants were placed in the chambers. Since not enough containers were available, the chambers had no surrounding plants. Leaf area was determined after the measurements. Two extra containers were harvested in the first week. Development of LAI during the measurements was estimated by non-linear interpolation.

The canopies were fumigated on two consecutive Tuesdays and Thursdays. SO_2 was supplied to one chamber from 8.00 h - 13.00 h and to the other one from 13.00 h - 20.00 h. Because of the expected variation in radiation conditions, the crops were fumigated with 800 μg SO_2 m^{-3} in all experiments. This concentration was based on preliminary experiments.

Dynamic simulation of SO_2 effects on canopy photosynthesis. In order to compare simulated effects of SO_2 on canopy photosynthesis with measurements, photosynthesis of a block-leaf canopy was modelled by an adapted version of the procedure for the calculation of photosynthesis of row canopies, developed by Goudriaan (1977) and improved by Gijzen and Goudriaan (in prep.), which is basically identical to the procedure for the calculation of photosynthesis of horizontally homogeneous canopies given by Goudriaan (1982, 1986) and Spitters (1986).

The fraction of diffuse radiation was calculated according to Spitters, Toussaint and Goudriaan (1986), where it is related to the ratio between the observed global radiation and the calculated extra terrestrial global radiation. The solar position was calculated from the latitude and time of measurement (day and hour). The fraction of photosynthetically active radiation (400-700 nm) was assumed to be 50% of the global radiation. Absorption of light by the acrylic chamber was about 20%.

The path length of a single light beam from the margin of the block to a given point in the block canopy was calculated according to Goudriaan (1977) by using a converted co-ordinate system, to characterize the direction of the beam with respect to the spatial position of the block. By multiplying this path length by the leaf area density, it could be expressed as the leaf area traversed by the beam. The leaf area in the block was assumed to be homogeneously distributed over the block volume.

The average leaf projection in any direction was assumed to be 0.5 (spherical leaf angle distribution, Goudriaan (1977)). Taking into account reflection of the canopy, scattering by the leaves (transmission and reflection by the leaves in the canopy) and the path length, the radiation flux from a certain point at the hemisphere at a given point in the block, can be calculated. The absorbed radiation at a point in the canopy equals the radiation decrease in the direction of the beam. Integration of absorbed diffuse radiation over all angles of incidence, was performed with the Gaussian integration principle (Goudriaan, 1988). Calculation of absorption and scattering of direct radiation is analogous to the procedures given by Goudriaan (1982), Spitters (1986) and Spitters et al. (1986) for horizontally homogeneous canopies.

At a given point in the block canopy, SO_2 uptake, S(IV) oxidation and the amount of S(IV) in the leaf (influencing the rate of photosynthesis at light saturation) was calculated in a submodel for leaf photosynthesis according to Kropff (1989a, b). The rate of photosynthesis was calculated on the basis of the absorbed flux of radiation and the S(IV) concentration in the leaves at that point in the canopy. On the basis of earlier observations, effects on respiration were neglected (Kropff, 1987).

Total photosynthesis of the block was obtained by a 5-point Gaussian integration (Goudriaan, 1986) over length, width and height of the block. The rate of photosynthesis and the balance of S(IV) in the leaf at 125 points in the block was calculated every timestep of integration for sunlit (divided over 3 leaf angle classes) and shaded leaves separately. The model was run with a time interval of 1 minute.

Modelling the effects of SO_2 on daily canopy photosynthesis. Other approaches than the one described above which operate with timesteps of one minute, have to be used when submodels for the uptake and effects of SO_2 are included in crop growth simulation models with integration intervals of one day. In the existing simulation models for crop growth, daily photosynthesis of crop canopies is calculated from an assumed daily pattern for weather data, calculated from daily totals (radiation) or averages (temperature, rainfall) (Spitters et al., 1986). The rate of photosynthesis is calculated for a selected number of moments per day and integrated over the day by using the Gaussian integration principle, which enables a strong reduction of the number of calculations (Goudriaan, 1986). When the effects of air pollutants are included, processes with time coefficients of several minutes have to be approached with equilibrium models.

The basic equation for the calculation of daily canopy photosynthesis is the photosynthesis light response curve for individual leaves (Goudriaan, 1982), described by:

$$P = P_{\max} (1 - e^{-\varepsilon I / P_{\max}}) \qquad (1)$$

where P is the rate of leaf photosynthesis (g CO_2 m^{-2} s^{-1}), $P_{\max}$ is the rate of leaf photosynthesis at light saturation (g CO_2 m^{-2} s^{-1}), ε is the initial light use efficiency (g CO_2 J^{-1}) and I is the absorbed radiation (PAR J m^{-2} s^{-1}). It has been shown that SO_2 only influences the rate of photosynthesis at high levels of radiation (Black, 1982; Hållgren, 1984; Kropff, 1987). The effect of SO_2 on the maximum rate of photosynthesis is linearly related to the amount of toxic SO_2 metabolites in the mesophyll (S(IV) (mmol l^{-1}) when photosynthetic reduction is not extremely high (Kropff, 1989a):

$$P_{\max,s} = P_{\max,0} (1 - k\ \mathrm{S(IV)}) \qquad (2)$$

where $P_{\max,0}$ is the maximum rate of leaf photosynthesis in clean air, $P_{\max,s}$ is the maximum rate of leaf photosynthesis during exposure to SO_2, and k is the effect parameter (mmol S(IV) $l^{-1})^{-1}$.

Photosynthetic reduction stabilizes soon after the start of exposure of leaves to SO_2 (Black and Unsworth, 1979b; Kropff, 1987) which can be explained by a rapid establishment of equilibrium concentration of S(IV) in the leaf (Kropff, 1989a). The supply of new metabolites by SO_2 uptake (F, mmol m^{-2} s^{-1}) divided by leaf thickness (d in mm) then equals the rate of S(IV) removal by oxidation (which can be approached as a first order reaction with a time coefficient τ_2):

$$\frac{F}{d} = \frac{S(IV)}{\tau_2} \tag{3}$$

The combination of Eqns 2 and 3 gives an expression for the maximum rate of leaf photosynthesis during fumigation:

$$\frac{P_{\mathrm{max,\,s}}}{P_{\mathrm{max,\,0}}} = 1 - \frac{k\,\tau_2\,F}{d} \tag{4}$$

The sum of resistances to CO_2 (consisting of the stomatal- and boundary layer resistance, s m^{-1}) can be derived from the rate of leaf photosynthesis (P, g CO_2 m^{-2} s^{-1}) and the difference between ambient and internal CO_2 concentrations ($C_a - C_i$, g CO_2 m^{-3}), which tends to be constant at a given CO_2 concentration even during SO_2 exposure (Kropff, 1987):

$$r_s = \frac{C_a - C_i}{P} - r_b \tag{5}$$

The flux of SO_2 into the leaf (F, mmol SO_2 m^{-2} s^{-1}) can be calculated from the ambient SO_2 concentration (S_a mmol SO_2 m^{-3}) assuming the internal SO_2 concentration to be 0 (Black and Unsworth , 1979a; Carlson, 1983; Kropff, 1989a) and the stomatal (r_s) and boundary layer (r_b) resistance to SO_2 (r_s for SO_2 equals about 1.21 × r_s for CO_2 and r_b for SO_2 is about 1.13 × r_b for CO_2). The expession for the flux is:

$$F = \frac{S_a}{1.21\,r_s + 1.13\,r_b} \tag{6}$$

With the Eqns 1, 4, 5 and 6 the effect of SO_2 on leaf photosynthesis in equilibrium can be calculated. However, this has to be done iteratively, since there is an internal loop in the equations: photosynthetic rate determines the stomatal resistance and thus SO_2 uptake which reduces photosynthesis in turn.

Results and discussion

Measured SO_2 effects on canopy photosynthesis. Table 1 gives some data on the four enclosed crop canopies exposed to SO_2 on four days in April, 1988, under the following environmental conditions with varying leaf area indices. On 19 and 28 April the sky was almost continuously clear, while on 21 and 26 April the sky was cloudy, resulting in strongly fluctuating radiation levels (Fig. 1). The extremely high peak levels of radiation on 26 April were caused by reflecting white clouds. Due to occasional equipment failure, radiation data were not always logged. Relative humidity in the chambers varied between 36 and 47%.

Net photosynthesis measured in the two chambers on 19 April is given in Fig. 2. Both the LAI and photosynthesis of the crops in both chambers was almost equal (Table 1). The effect of SO_2 fumigation was only detectable around noon, when photosynthetic rates were high. In the morning, when chamber 2 was fumigated, photosynthesis was

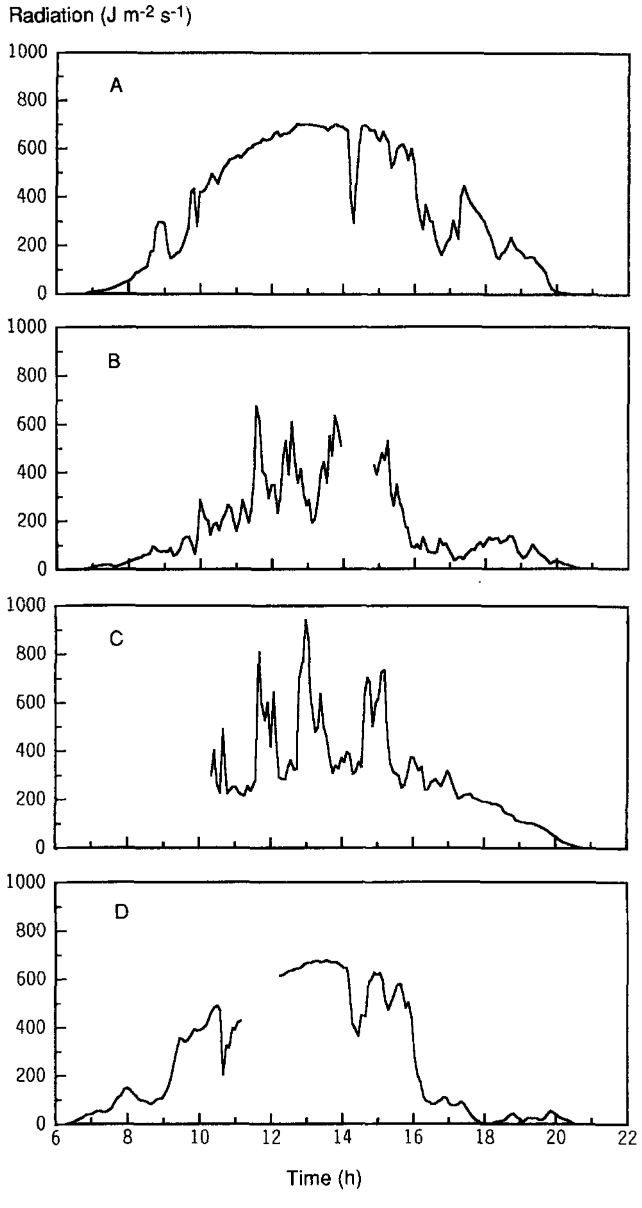


Fig. 1. Diurnal time course of total global radiation (J m^{-2} s^{-1}) during fumigation experiments (A) 19 April; B) 21 April; C) 26 April; D) 28 April). No data were available for some periods due to equipment failure.

lower than photosynthesis in chamber 1. After fumigation was switched to chamber 1 at noon, photosynthesis in chamber 2 became higher than photosynthesis in chamber 1. Fig. 2 clearly illustrates that the SO_2 effect was smaller in periods with low photosynthesis and reduced radiation levels due to clouds (i.e. at 14.00 h, Fig. 1A). These

Table 1. Environmental conditions and leaf area indices (LAI) of 4 *Vicia faba* canopies during the fumigation experiments in 1988 at Wageningen.

Date	19 April	21 April	26 April	28 April
Daily total radiation (MJ m^{-2} d^{-1})	16.15	8.87	16.80	14.71
Hours sunshine	7.3	0.9	5.9	4.7
Relative humidity (inside chamber)	47	39	36	39
LAI chamber 1	1.6	1.8	1.9	2.1
LAI chamber 2	1.6	1.8	2.1	2.3
Chamber fumigated in the morning	2	1	1	2
Chamber fumigated in the afternoon	1	2	2	1

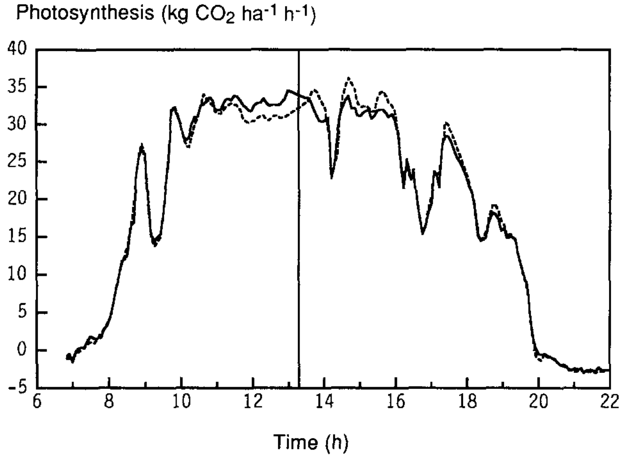


Fig. 2. Diurnal canopy photosynthesis (kg CO_2 ha^{-1} h^{-1}) on 19 April during SO_2 exposure. Chamber 2 (--------) was fumigated in the morning and chamber 1 (———) was fumigated in the afternoon. Moment of fumigation switch between the chambers is indicated with a vertical line.

results are consistent with experimental data on the effects of SO_2 on leaf and plant photosynthesis, which indicate effects on photosynthesis at light saturation only (Black, 1982; Hållgren, 1984; Kropff, 1987).

The rates of photosynthesis from 10.00 h - 16.00 h on the four measurement days are given in Fig. 3 for the period around the fumigation switch. In the second week the crop in chamber 2 had a higher LAI than the crop in chamber 1 resulting in higher rates of photosynthesis. To enable graphical comparison of the data of both chambers, the rate of photosynthesis in chamber 2 was corrected for this difference in LAI by scaling with the mean ratio between photosynthesis of chamber 2 and chamber 1 (determined by linear regression). The effect of fumigation was clearly observed on 19 and 28 April, when the sky was clear for a long period. Canopy photosynthesis was reduced by about 6% on 19 April and by about 4% on 28 April by fumigation with 800 μg SO_2 m^{-3}.

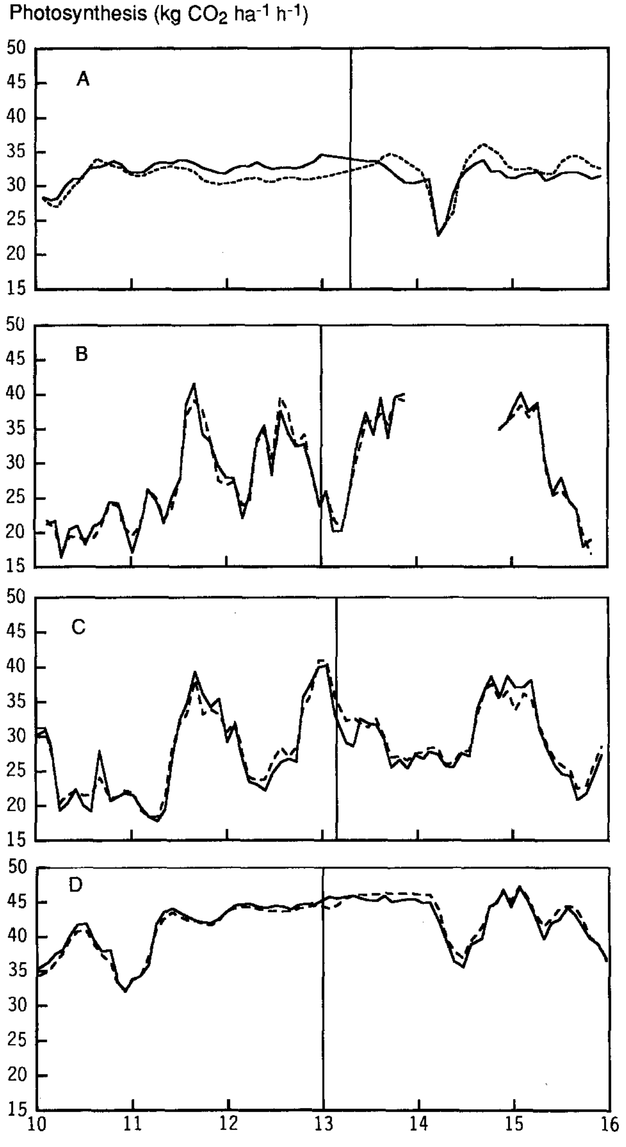


Fig. 3. Canopy photosynthesis (kg CO_2 ha^{-1} h^{-1}) from 10.00 h to 16.00 h during fumigation experiments (A) 19 April; B) 21 April; C) 26 April; D) 28 April). Moment of fumigation switch between the chambers is indicated by a vertical line. Chamber 1 (————) was fumigated in the mornings and chamber 2 (--------) in the afternoons on 21 and 26 April. Chamber 2 was fumigated in the morning and chamber 1 in the afternoon on 19 and 28 April.

No effects of SO_2 on canopy photosynthesis were detected on 21 and 26 April when radiation continual changed. However, interpretation of these results was difficult as a result of the time lag between gas analysis of the chambers (72 seconds) and the

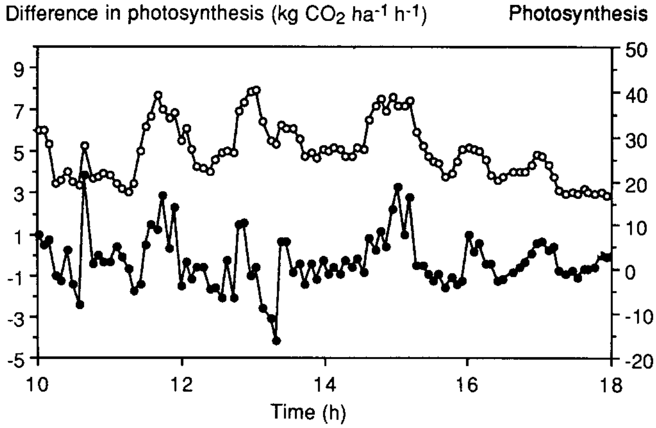


Fig. 4. Canopy photosynthesis in chamber 1 (kg CO_2 ha^{-1} h^{-1}) (○) and the difference in photosynthesis between both chambers (kg CO_2 ha^{-1} h^{-1}) (●) on 26 April during SO_2 exposure.

sampling interval of data by the computer (5 minutes). When radiation and photosynthesis quickly changed, the difference between photosynthesis of the two chambers fluctuated. This effect is illustrated in Fig. 4, where both the rate of photosynthesis of one of the enclosed canopies and the difference in the rate of photosynthesis between the chambers on 26 April is plotted. The difference between 1 and 2 was positive when photosynthesis increased, because chamber 2 was sampled first and was negative when photosynthesis decreased. The only periods when photosynthesis was more or less stable for 2 subsequent measurements at high radiation levels was on 26 April at 13.00 h, when chamber 1 was fumigated and around 15.00 h when chamber 2 was fumigated. The pattern in photosynthetic reduction during these periods confirms the effects observed on the clear days.

The conductance of the canopy appeared to follow the assimilation rate with a delay

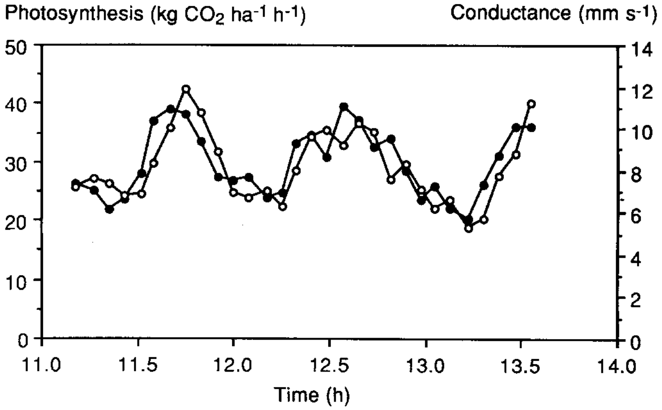


Fig. 5. Time course of canopy photosynthesis (kg CO_2 ha^{-1} h^{-1}) (●) and canopy conductance (mm s^{-1}) (○) on 21 April.

of 5 minutes (Fig. 5). A similar delay with respect to photosynthesis was observed by Goudriaan, Louwerse and Van Kleef (in prep.) for Faba bean crops. This is of importance for the uptake of SO_2 by leaf canopies when radiation fluctuates, since the uptake of SO_2 and the pool of SO_2 metabolites will also follow photosynthesis with a delay. When radiation fluctuates, highest S(IV) levels will occur when photosynthesis is already lower and will thus have less influence on photosynthesis.

Model performance. The time course of photosynthesis in both chambers was simulated for the four days on which the crops were exposed to about 800 μg SO_2 m^{-3} for half a day. The measured data on radiation and SO_2 concentration were input in the model, of which the model parameters are listed in Table 2. The time course of photosynthesis of the enclosed crops on all four days was accurately simulated with the model (Fig. 6), where the observed and simulated photosynthesis in chamber 1 is plotted for a clear (19 April) and a cloudy day (21 April). Because the effects of SO_2 were very small, the accuracy of simulation of the effects of SO_2 can best be analysed by plotting the simulated and observed difference in photosynthesis between the chambers. The measured differences on the cloudy days cannot be interpreted due to the delay of 72 seconds between the measurements of the chambers, which causes strong fluctuations in the difference in photosynthesis between the chambers (see Fig. 4). Therefore only the results for the 2 clear days (19 and 28 April) are given in Fig. 7. For the construction of Fig. 7B (28 April) the data on measured and simulated photosynthesis of chamber 2 were corrected for differences in LAI. The time course of the difference in photosynthesis between the chambers was simulated very well on the basis of effect parameters derived in earlier studies of the effects of SO_2 on leaf photosynthesis (Table 1; Kropff, 1989b). The magnitude of the effect was simulated correctly on 19 April, but was slightly overestimated on 28 April. This may have been caused by the different conditions at which the plants had been grown before the measurements started. The plants which were measured in the first week had been grown outdoors for one week at daily average temperatures of 10 °C and the plants measured in the second week had been grown outdoors for two weeks at high radiation levels and low temperatures (daily average temperature of about 5 °C in the second week when the first crop was measured). This resulted in thicker leaves of the second group of plants (0.5 mm compared to 0.4 mm). This effect was accounted for in the model.

Table 2. Parameters used in the simulation model for the effects of SO_2 on canopy photosynthesis.

C_i/C_a (−)	0.75
P_{max} (g CO_2 m^{-2} s^{-1})	8.3×10^{-4}
Initial light use efficiency (g CO_2 J^{-1})	12.5×10^{-6}
Sensitivity parameter k ((mmol S(IV) $l^{-1})^{-1}$)	0.9
Leaf thickness (mm)	0.4-0.5*
Time coefficient for S(IV) oxidation (minutes)	20
Time coefficient for reaction of stomata (minutes)	5

* Leaf thickness of the plants in the first week was 0.4 mm and in the second week 0.5 mm.

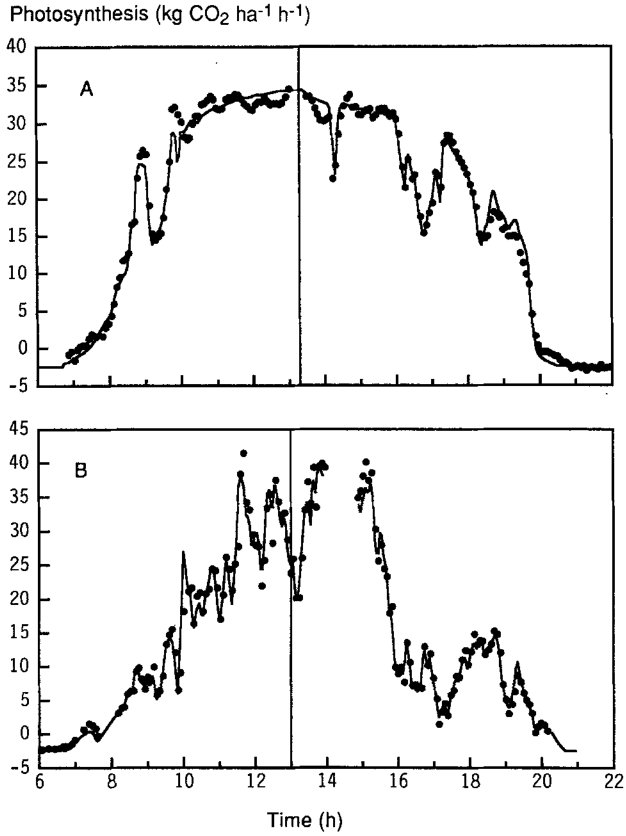


Fig. 6. Simulated (–) and observed (●) diurnal canopy photosynthesis (kg CO_2 ha^{-1} h^{-1}) on 19 April (A) and 21 April (B) in chamber 1.

Effect of SO_2 on daily photosynthesis of canopies. To analyse the errors made by neglecting the effect of quick changes on S(IV) concentration in the leaf in equilibrium models, the time course of photosynthesis during SO_2 exposure on 19 April was simulated with both the detailed and the equilibrium approach for the block canopy. Fig. 8 shows that the effect of SO_2 is overestimated with the equilibrium approach when radiation of SO_2 concentration quickly changes, since delays in the processes determining the S(IV) pool in the leaf are ignored in the equilibrium approach. The difference between both versions of the model are small, especially when compared to the actual rates of canopy photosynthesis. The overestimation of the effect will be strongest on days in which radiation strongly fluctuates. The equilibrium approach should be used in models operating with timesteps of integration of one day and require daily total radiation as input. It should be noted that this overestimation of effects, when radiation fluctuates, will be compensated by the underestimation of effects during bright periods, because daily total radiation is smoothly distributed over the day in these models.

The simulated uptake of SO_2 by a normal crop canopy (no block form) and its effect on gross canopy photosynthesis in dependence of daily global radiation at 800 μg

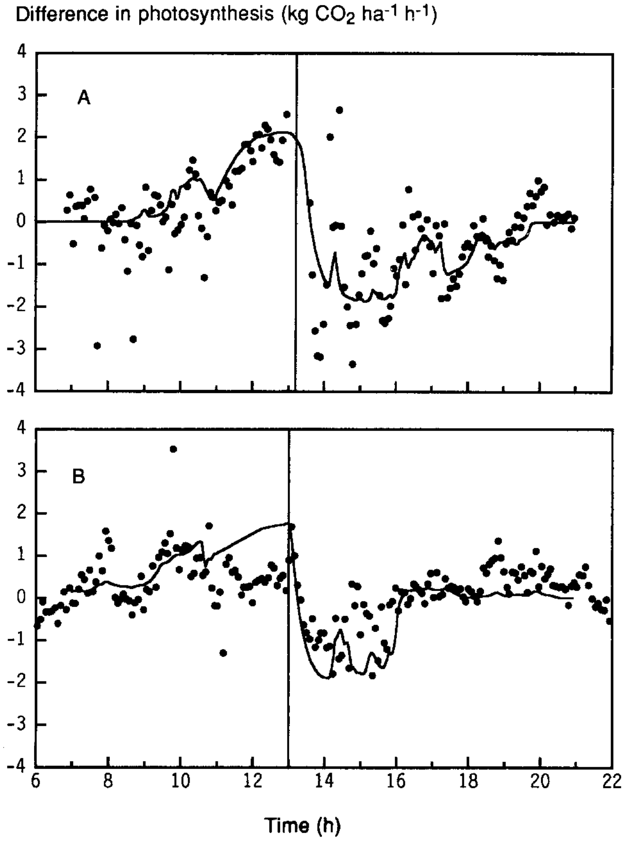
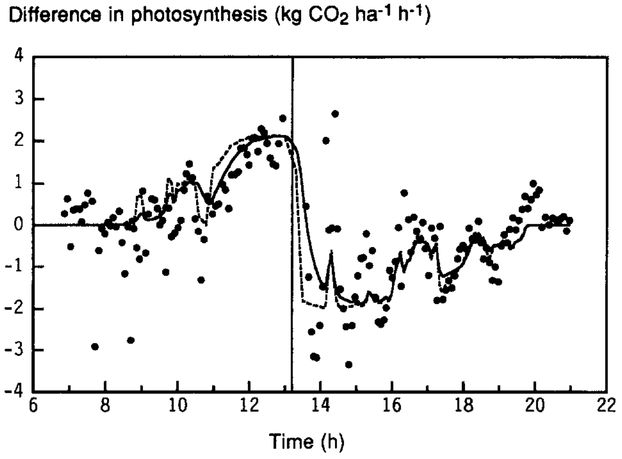


Fig. 7. Simulated (–) and observed (●) difference in diurnal canopy photosynthesis (kg CO_2 ha^{-1} h^{-1}) between both chambers on 19 April (A) and 28 April (B). On both days chamber 2 was fumigated in the morning and chamber 1 in the afternoon. Moment of fumigation switch between the chambers is indicated by a vertical line.



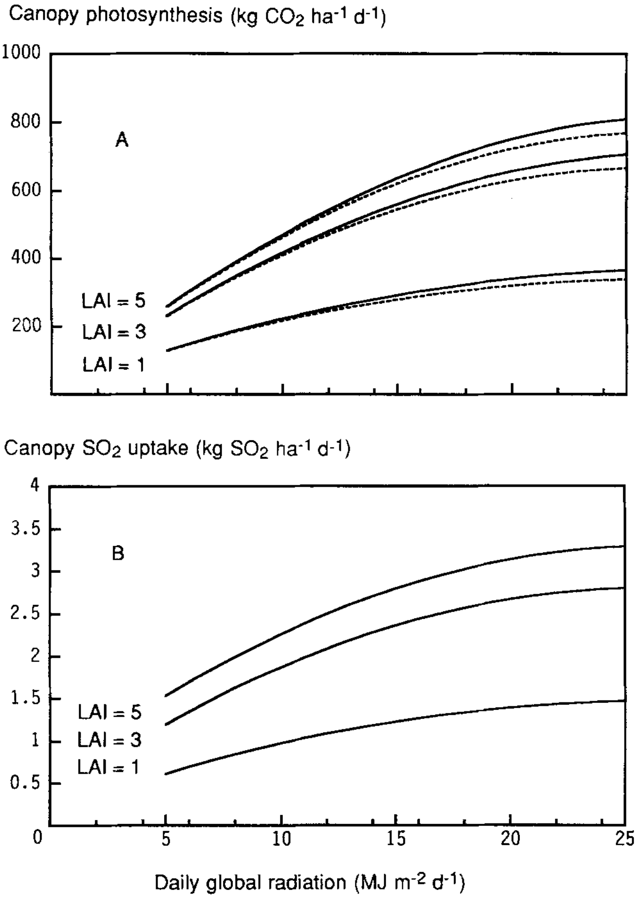


Fig. 9. A) Simulated relation between canopy gross photosynthesis and daily global radiation for an LAI of 1, 3 and 5 respectively, without SO_2 (–) and with 800 μg SO_2 m^{-3} (---) and B) Simulated relation between SO_2 uptake by the canopy and daily global radiation. Parameters for Faba beans (see text).

SO_2 m^{-3} is presented in Fig. 9 (for the maximum rate of leaf photosynthesis $P_{max,0}$ the value of 0.0011 g CO_2 m^{-2} s^{-1} was used, since this is more realistic for field grown plants). This figure clearly shows that effects on daily canopy photosynthesis only occurred at high radiation levels, and hardly increased with LAI. Since canopy conductance is closely correlated to the rate of photosynthesis, the daily uptake of SO_2 by the canopy followed the same pattern as the rate of photosynthesis. Fig. 10 shows that the relative effect of SO_2 on canopy photosynthesis was smaller at higher LAI, because

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Fig. 8. Simulated and observed difference in diurnal canopy photosynthesis (kg CO_2 ha^{-1} h^{-1}) between both chambers on 19 April with the detailed version of the model (–) and the equilibrium approach (---). Moment of fumigation switch between the chambers is indicated by a vertical line.

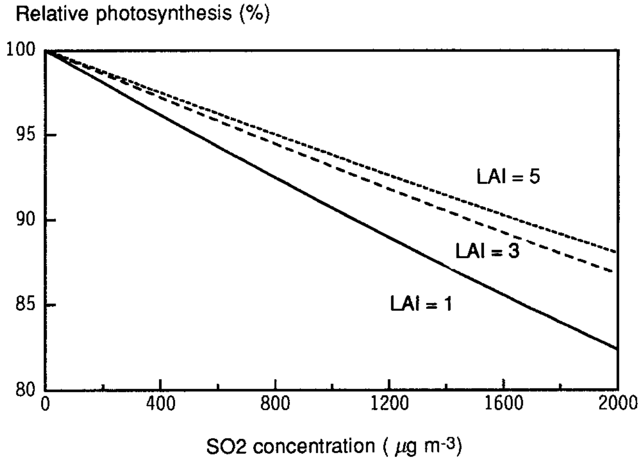

Fig. 10. Simulated effect of SO_2 on relative gross canopy photosynthesis at an LAI of 1, 3 and 5 respectively, on a clear day in June. Parameters for Faba beans (see text).

more leaves were functioning at low levels of radiation. The effect of SO_2 on canopy photosynthesis was smaller than the effect of SO_2 on leaf photosynthesis (for the same conditions Kropff (1989b) observed a reduction of 10%). This is caused by changes in the maximum rate of photosynthesis on single leaves and canopies. Only few leaves function at high radiation levels in leaf canopies. Most leaves are shaded by other leaves. Only photosynthesis of sunlit leaves will be affected by SO_2.

The effects presented in Figs 9 and 10 are small. When the plants are more sensitive (thinner leaves, larger time coefficient for S(IV) oxidation) these effects are stronger. Table 3 shows the effect of SO_2 on daily canopy photosynthesis for leaf canopies, differing in average leaf thickness (0.2-0.4 mm) and the time coefficient for S(IV) oxidation. Two realistic extreme values are chosen: 20 minutes and 100 minutes (Kropff, 1989b). Considerable effects on leaf canopy photosynthesis are only observed at the high SO_2 concentration of 800 $\mu g\ SO_2\ m^{-3}$, even when the leaves are very sensitive (thin leaves and a slow rate of S(IV) oxidation). These results explain the findings of several workers who studied the effect of SO_2 on crop growth in field situations, and observed

Table 3. Simulated effect of SO_2 on daily canopy photosynthesis (in % reduction) on a clear day in May in the Netherlands for two crops with a LAI of 5 and an average leaf thickness of 0.4 and 0.2 mm respectively, and with two different time coefficients for S(IV) oxidation (τ_2 = 20 and 100 minutes, respectively).

	Leaf thickness 0.4 mm		Leaf thickness 0.2 mm	
	$\tau_2 = 20$	$\tau_2 = 100$	$\tau_2 = 20$	$\tau_2 = 100$
100 $\mu g\ SO_2\ m^{-3}$	0.4	2.3	1.0	4.6
800 $\mu g\ SO_2\ m^{-3}$	3.6	17.8	7.3	31.5

no effects on crop growth in the linear growth phase of the crop at concentrations < 150 μg SO_2 m^{-3} (Baker et al., 1986; McLeod et al., 1988; Kropff et al., in prep.). The small effects of low SO_2 concentrations on crop growth during winter may be explained by differences in the oxidation characteristics at low temperatures. More research on the effects of environmental factors and plant characteristics on the time coefficient for S(IV) oxidation is required to predict effects in extreme winter conditions.

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Samenvatting

Simulatie van de korte termijn effecten van zwaveldioxide. 3. Effecten van SO_2 op de gewasfotosynthese

Het effect van SO_2 op de fotosynthese van een tuinbonengewas is gemeten met mobiele apparatuur. Gewasfotosynthese werd alleen beïnvloed (4-6% reductie) bij hoge stralingsnivo's tijdens begassing met 800 μg SO_2 m^{-3}.

De experimentele gegevens zijn gebruikt om een model voor de effecten van SO_2 op de gewasfotosynthese te evalueren. Het model bestaat uit een rekenprocedure voor de fotosynthese van gewassen dat is uitgebreid met een submodel voor de opname en effecten van SO_2 op de fotosynthese van bladeren. De dagelijkse gang van de fotosynthese en de effecten van SO_2 op de fotosynthese werden nauwkeurig gesimuleerd met het model. Mogelijkheden voor de toepassing van het model in gewasgroeimodellen, die met een tijdstap van één dag werken, wordt gepresenteerd en geëvalueerd.

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