Physiological effects of sulphur dioxide.

1. The effect of $SO_2$ on photosynthesis and stomatal regulation of *Vicia faba* L.

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**Abstract.** The effect of short-term $SO_2$ fumigation on photosynthesis and transpiration of *Vicia faba* L. was measured at different irradiances and $SO_2$ concentrations. At high irradiances photosynthetic rates were reduced when leaves were exposed to $SO_2$, and the magnitude of the reduction was linearly related to the rate of $SO_2$ uptake through the stomata. Photosynthetic rates stabilized within 2 h after the start of fumigation.

The effect of $SO_2$ on photosynthesis was measured at different $CO_2$ concentrations to analyse the contribution of stomatal and non-stomatal factors to photosynthetic inhibition. Mesophyll resistance to $CO_2$ diffusion increased as a result of $SO_2$ exposure and caused a rapid reduction in photosynthesis after the start of fumigation. Stomatal resistance was not affected directly by $SO_2$ fumigation, but indirectly as a result of a feedback loop between net photosynthesis and internal $CO_2$ concentration.

Analysis of gas-exchange measurements in biochemical terms indicated that photosynthetic inhibition during $SO_2$ exposure can be explained by a stronger reduction in the affinity of RBP carboxylase/oxygenase for $CO_2$ than for $O_2$.

**Key-words:** *Vicia faba*; Papilionaceae, broad bean; photosynthesis; stomatal behaviour.

**Introduction**

Sulphur dioxide is one of the major gaseous air pollutants that cause damage to agricultural crops and natural vegetation. Exposure of plants to high concentrations of $SO_2$ can cause chlorosis and necrosis of leaf tissue, which lead to reductions in growth. Reduced plant growth in the absence of visible injury has also been observed at relatively low ambient $SO_2$ concentrations (Lockyer, Cowling & Jones, 1976; Ashenden & Mansfield, 1977; Sprugel et al., 1980). The magnitude of $SO_2$-induced effects on plant growth depends not only on pollutant concentration but also on plant status (physiological status is dependent on plant age, growing conditions like nutrient availability, water supply, irradiance and temperature) and microclimatic factors (Black, 1982; Hällgren, 1984).

The rate of photosynthesis at light saturation appears to be negatively correlated with the rate of uptake of $SO_2$ through the stomata (Black & Unsworth, 1979b; Winner & Mooney, 1980a,b; Black, 1982; Carlson, 1983). Photosynthetic light use efficiency is not influenced by $SO_2$ (Black & Unsworth, 1979b; Hällgren & Gezelius, 1982). As the stomata are the primary sites where $SO_2$ enters the leaf tissue, much research has concerned the effect of $SO_2$ on stomatal resistance. Both stomatal opening and closure have been observed at low concentrations of $SO_2$. At high $SO_2$ concentrations only stomatal closure has been observed (Black, 1982). Environmental factors such as windspeed, humidity and light intensity have a strong effect on stomatal responses to $SO_2$ (Black & Unsworth, 1979a). In recent studies, attempts have been made to separate $SO_2$-induced effects on photosynthesis into stomatal and non-stomatal components. Non-stomatal factors (e.g. an increase in mesophyll resistance) appear to be primarily responsible for the reduction in photosynthesis (Barton, McLaughlin & McConathy, 1980; Winner & Mooney, 1980b). No consistent effects of $SO_3$ on dark respiration rates have been found. Both stimulation and inhibition of dark respiration have been observed at low $SO_2$ concentrations (Black, 1984). Ziegler (1975) concluded on the basis of *in vitro* studies, that the biochemical mechanism of inhibition of net photosynthesis by $SO_2$ is competition between $SO_2$ and $CO_2$ for binding sites on the carboxylating enzyme RBP carboxylase/oxygenase. Gezelius & Hällgren (1980), however, suggested a non-competitive or a mixed effect from *in vitro* measurements with pine chloroplasts.

In the present study the short-term effects of $SO_2$ on photosynthetic characteristics of *Vicia faba* leaves are analysed by making a time-dependent distinction between stomatal and non-stomatal components of photosynthetic changes. The results of the $CO_2$ gas exchange measurements are also interpreted in biochemical terms in an effort to relate these results to published results of *in vitro* measurements.
Materials and methods

Plant material and experimental system

Plants of *Vicia faba* (cv. minica) were grown in 11-cm diameter plastic pots filled with a commercial potting mixture in a greenhouse at an average temperature of 16°C and about 50% relative humidity. Supplementary illumination provided a photoperiod of 16 h. The soil-moisture level was maintained at field capacity. CO₂ assimilation measurements were started when the plants were flowering and had about 14 pairs of leaflets. The sulphur content of the leaves was 7.7 ± 0.6 mg S g⁻¹.

Rates of CO₂ assimilation, respiration and transpiration of the youngest fully unfolded leaflet were measured with equipment for routine measurements of photosynthesis comparable to the type described by Louwerse & van Oorschot (1969). SO₂ was supplied from a cylinder (1000 ppm SO₂ in N₂) through a flowmeter and was injected into the air supply of the leaf chamber. Gas samples from the air lines leaving the chambers were drawn continuously through teflon tubing and analysed with a Philips SO₂ gas analyzer (type PW 9700). Relative humidity in the leaf chamber was about 40–50% and air temperature was 23°C. The incoming SO₂ flow was continuously adjusted to prevent large changes in SO₂ concentration in the leaf chamber.

Calculations and experimental procedure

Data on differences in CO₂ concentration and water vapour content of the air stream entering and leaving the leaf chambers, temperature, irradiance and air humidity were recorded every 5 min by a micro-computer. SO₂ concentration was also monitored. Measurements were performed during a pre-fumigation period of 2 h to obtain stable rates, during a subsequent SO₂ fumigation period of 2 h, and finally during a dark period of 1 h. Rates of net photosynthesis and transpiration, stomatal resistance and internal CO₂ concentration were calculated following the procedure of Goudriaan & van Laar (1978), in which stomatal resistance to CO₂ is calculated from the transpiration rate and corrected for differences in diffusion coefficients between CO₂ and H₂O. Internal CO₂ concentration (Ci) is computed with the resistance model for CO₂ diffusion through the stomata from the rate of photosynthesis (Pn), external CO₂ concentration (Ce), stomatal resistance (rs) and the experimentally determined boundary layer resistance (rb): Ci = Ce - Pn(rs + rb). The flux of SO₂ into the leaf interior was calculated by dividing the SO₂ concentration in the leaf chamber by the sum of the calculated stomatal resistance and an experimentally determined boundary layer resistance (about 7 s m⁻¹) for SO₂. The SO₂ concentration at internal leaf surfaces was assumed to be zero. This is a reasonable assumption because the resistance for SO₂ going into solution at the wet surface of the stomatal cavity is very low during short exposures (Unsworth, Biscoe & Black, 1976; Black & Unsworth, 1979a; Carlson, 1983). Since the cuticular resistance for SO₂ is extremely high compared to stomatal resistance, the flux of SO₂ through the cuticula is negligible (Unsworth et al., 1976).

Three series of measurements were performed. In series 1 the effect of fumigation with 400 μg SO₂ m⁻³ on photosynthesis was measured at irradiances (visible 400–700 nm) ranging from 0–300 J m⁻² s⁻¹ at a constant ambient CO₂ concentration of 340 ppm to analyse the effect of SO₂ on the photosynthesis-light-response characteristics of leaves. The CO₂ assimilation-light-response curve for individual leaves can be described by a negative exponential function (Goudriaan, 1982):

\[ P_n = (P_{max} + R_d)(1 - \exp (-I/\Gamma)) - R_d, \]

where

- \( P_n \) = net CO₂ assimilation rate (\( \mu \)g CO₂ m⁻² s⁻¹),
- \( P_{max} \) = CO₂ assimilation rate at light saturation (\( \mu \)g CO₂ m⁻² s⁻¹),
- \( R_d \) = dark respiration rate (\( \mu \)g CO₂ m⁻² s⁻¹),
- \( I \) = absorbed radiation (J m⁻² s⁻¹),
- \( \Gamma \) = initial light-use efficiency (\( \mu \)g CO₂ J⁻¹).

The parameters \( P_{max} \), \( R_d \) and \( \Gamma \) were determined by using an optimization programme.

In the second series of measurements the effect of SO₂ concentrations ranging from 0–800 μg SO₂ m⁻³ on photosynthesis was measured at light saturation (300 J m⁻² s⁻¹) and a CO₂ concentration of 340 ppm.

In the third series of measurements the effect of a single concentration of SO₂ (800 μg m⁻³) on photosynthesis was measured at light saturation (300 J m⁻² s⁻¹) and CO₂ concentrations ranging from 30–850 ppm CO₂. The confounding effect of differences in stomatal resistance was eliminated by relating the CO₂ assimilation rate to internal CO₂ concentration. This relationship can be described mathematically as (J. Goudriaan, personal communication):

\[ P_n = P_{max} (1 - \exp (-g_m(C_i - \Gamma)/P_{max})), \]

where

- \( P_n \) = net CO₂ assimilation rate (\( \mu \)g CO₂ m⁻² s⁻¹),
- \( P_{max} \) = net CO₂ assimilation rate at CO₂ saturation (\( \mu \)g CO₂ m⁻² s⁻¹),
- \( C_i \) = internal CO₂ concentration (\( \mu \)g CO₂ m⁻³),
- \( \Gamma \) = CO₂ compensation point (\( \mu \)g CO₂ m⁻³),
- \( g_m \) = mesophyll conductance (m s⁻¹).

The mesophyll resistance to CO₂ is the inverse of the mesophyll conductance \( g_m^{-1/dim} \) dimension s m⁻¹).
SO$_2$, PHOTOSYNTHESIS AND STOMATAL REGULATION

Separation of stomatal and non-stomatal effects

The effect of SO$_2$ on the mesophyll resistance to CO$_2$ can be analysed by fitting eqn (2) to data on net photosynthesis at different CO$_2$ concentrations. Equation (2) cannot be used to analyse the effect of SO$_2$ on stomatal resistance because it relates photosynthesis to the internal CO$_2$ concentration. Several methods have been developed to quantify the relative importance of mesophyll and stomatal components to a change in photosynthetic rate during stress situations (Jones, 1985; Rabbinge, Jorritsma & Schans, 1985). Winner & Mooney (1980b) showed that both components contribute to a reduction in photosynthetic rates after fumigation, but did not analyse their relative contributions during the fumigation period. When both components are responsible for changes in photosynthesis their relative effects are 'path dependent' (Jones, 1985), which makes it necessary to analyse the time course of photosynthesis and C; during fumigation. This is illustrated in Fig. 1. If the stomatal resistance increases, the internal CO$_2$ concentration will drop, so that the photosynthetic rate will be reduced according to the photosynthesis-C$_i$ curve (trajectory A-A$_1$). If the mesophyll resistance to CO$_2$ increases and stomatal resistance remains unchanged, C$_i$ will increase according to the dotted line (trajectory A-A$_1$), representing the so-called 'supply function': a linear resistance model for CO$_2$ diffusion into the stomatal cavities. If both the stomatal and mesophyll resistance increase (A-A$_2$), the trajectory will be A-A$_2$-A$_3$ when stomata close first (relative contribution of the stomatal component is (A-A$_2$)/A-A$_3$), and will be A-A$_1$-A$_3$ when the mesophyll resistance increases first (relative contribution of the stomatal component is (A$_1$-A$_3$)/A-A$_3$).

If a stress factor induces an increase in mesophyll resistance first, stomatal closure may subsequently occur as the result of the feedback loop between photosynthesis and stomatal resistance. This feedback loop results in a constant ratio between C$_i$ and C$_s$ (the ambient CO$_2$ concentration) which is about 0.7 for C$_3$ plants (Goudriaan & van Laar, 1978; Bell, 1982; Farquhar & Sharkey, 1982). This constant ratio can be used to describe stomatal behaviour in simulation models for crop growth. Stomatal resistance can then be calculated from the rate of photosynthesis using the resistance model for CO$_2$ diffusion through the stomata:

\[ r_s = \frac{C_n - C_i}{P_n - r_b}, \]

where $r_b$ is the boundary layer resistance to CO$_2$, and $r_s$ is the stomatal resistance. This procedure can be used for the calculation of canopy transpiration (Goudriaan, 1977; de Wit et al., 1978; Goudriaan, 1982) and can be used for the calculation of SO$_2$ uptake, when SO$_2$ does not alter stomatal behaviour. Any influence of SO$_2$ on stomatal behaviour will be reflected in the $C_i/C_n$ ratio.

Biochemical interpretation of gas exchange measurements

The hyperbolic Michaelis–Menten equation can be used to analyse the biochemical mechanism of SO$_2$ inhibition of net photosynthesis with in vivo data on leaf photosynthesis at varying CO$_2$ concentrations (Edwards & Walker, 1983):

\[ V = \frac{V_o(C_i - \Gamma)}{C_i + K_o + \frac{[O]}{K_o}}, \]

where $V$ is the net photosynthetic rate, $V_o$ is the photosynthetic rate at high CO$_2$ concentration, $\Gamma$ is the CO$_2$ compensation point, $K_o$ is the Michaelis constant for binding of CO$_2$ to RBP carboxylase/oxygenase, $K_s$ is the inhibition constant due to O$_2$ competition and [O] is the oxygen concentration in the leaf. An expression for the mesophyll resistance (the inverse of the initial slope at the CO$_2$ compensation point) can be derived from this equation:

\[ r_m = \frac{\Gamma + K_o}{V_o} \left( 1 + \frac{[O]}{K_o} \right). \]

The CO$_2$ compensation point also can be interpreted in biochemical terms by means of the Michaelis–Menten equations for carboxylation and oxygenation (Laing, Ogren & Hageman, 1974):

\[ \Gamma = t \frac{V_o K_o [O]}{V_o K_o}, \]

where $t$ is the fraction of glycolate carbon released (0.5) and $V_o$, the maximum rate of oxygenation.

![Figure 1. Partitioning of stomatal and non-stomatal contributions to a change in net photosynthesis. When stomatal resistance changes first the trajectory will be A-A$_1$-A$_2$; when the mesophyll resistance changes first the trajectory will be A-A$_1$-A$_3$, the dotted lines represent the supply functions ($C_i = C_n - A(r_s + r_b)$) where $r_s$ and $r_b$ are the stomatal- and boundary layer resistance response), with a slope of $-1/(r_s + r_b)$. Solid lines represent the response of photosynthesis to varying internal CO$_2$ concentrations for control plants (1) and for stressed plants (2). After Jones (1985).](image-url)
If the mechanism of inhibition of net photosynthesis by SO₂ is competition between SO₂, CO₂ and O₂ for the binding sites of the RBP carboxylase/oxygenase, as suggested by Ziegler (1975), then the mesophyll resistance should increase as a result of SO₂ fumigation:

\[ r_m = \frac{\Gamma + K_x}{V_e} \left( \frac{[O]}{K_o} + \frac{[S]}{K_s} \right), \]  

where [S] is the concentration of sulphur metabolites in the cells and Kₙ is the inhibition constant. The CO₂ compensation point, however, should remain unchanged.

**Results and discussion**

Inhibition of net photosynthesis in plants exposed to high concentrations of SO₂ has been reported by many researchers, but the effect of lower, more realistic concentrations (<0.1 ppm) has seldom been analysed (Black, 1982).

A typical time-response curve of net photosynthesis of fumigated and control plants at light saturation is shown in Fig. 2. A strong decrease in net photosynthesis of the fumigated plants occurred within the first 20 min of exposure to SO₂ and stable rates were obtained within 2 h. This pattern is in agreement with the results of Sij & Swanson, 1974; Black & Unsworth, 1979b; Barton et al., 1980; Sisson, Booth & Throneberry, 1981; Darrall, 1986). Because steady photosynthetic rates were obtained after a short fumigation period, it can be concluded that the concentration of toxic intermediate oxidation metabolites (sulphite, bisulphite) also reached stable values. These values depend upon the rate of uptake of SO₂ and the rates of oxidation of dissolved SO₂ to sulphate and the subsequent metabolites (Black & Unsworth, 1979b).

The CO₂ assimilation light–response curve was significantly affected by SO₂ fumigation. The fit of eqn (1) to the data is presented graphically in Fig. 3 and the estimated parameter values for photosynthetic rate at light saturation (Pₘₐₓ, dark respiration (R₉), and initial light use efficiency (φ) are given in Table 1. The estimated value of Pₘₐₓ decreased by 15% as a result of 2 h of fumigation with 400 µg SO₂ m⁻³ (P < 0.1). Estimated dark respiration (R₉) increased as a result of fumigation with SO₂ but not significantly. The initial light use efficiency (φ) was not affected by SO₂ fumigation. The effect of SO₂ on the photosynthesis light–response curve of individual leaves (Fig. 3) was similar to that found for whole plants of *Vicia faba* (Black & Unsworth, 1979b). However, Black & Unsworth (1979b) found a much stronger effect of SO₂ on dark respiration rates. The difference may be explained by increased respiration in organs other than leaves. Contradictory reports on the effect of SO₂ on dark respiration in a number of studies (reviewed by Black, 1984) indicate the need for more detailed research. The absence of an effect of SO₂ on initial light use efficiency has also been observed by Hälgren & Gezelius (1982) for pine seedlings.

The effect of SO₂ on photosynthesis at light saturation was analysed in relation to the calculated flux of SO₂ into the leaf interior at the end of the fumigation period instead of the external SO₂ concentration. The rate of CO₂ assimilation after 2 h of fumigation, relative to pre-fumigation rates, decreased linearly as the rate of SO₂ uptake

**Table 1. Estimated parameter values (±SE) of CO₂ assimilation at light saturation (Pₘₐₓ), the initial light use efficiency (φ) and dark respiration (R₉) before and after fumigation with 400 µg SO₂ m⁻³ (n = 49)**

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<th>After</th>
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<tr>
<td>Pₘₐₓ (µg CO₂ m⁻² s⁻¹)</td>
<td>724 ± 21</td>
<td>615 ± 15</td>
</tr>
<tr>
<td>φ (µg CO₂ J⁻¹)</td>
<td>13.9 ± 1.4</td>
<td>14.0 ± 1.3</td>
</tr>
<tr>
<td>R₉ (µg CO₂ m⁻³ s⁻¹)</td>
<td>40.5 ± 11.8</td>
<td>48.8 ± 10.2</td>
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increased from 0 to 1.5 \mu g m^{-2} s^{-1} (Fig. 4). This relation is very similar to that reported by Black & Unsworth (1979c) over the range of rates employed here, but they found no further reduction in photosynthesis at higher rates of SO₂ uptake (>1.5 \mu g m^{-2} s^{-1}). The reduction appeared to be reversible since prefumigation rates of photosynthesis were obtained when plants which had been fumigated with 800 \mu g SO₂ m^{-3} were measured after a 2-h recovery period without fumigation.

The ratio of \CO₂ assimilation to transpiration was not significantly affected by SO₂ fumigation (Table 2). The simultaneous reduction of \CO₂ assimilation and transpiration may have been caused either directly by an increase in stomatal resistance or indirectly by an increase in mesophyll resistance.

The effect of fumigation with 800 \mu g SO₂ m^{-3} on \CO₂ assimilation at light saturation and varying \CO₂ concentrations is shown in Fig. 5. The estimated parameter values for the photosynthetic rate at high \CO₂ concentrations (P_{max}), the mesophyll conductance (g_m) and the \CO₂ compensation point (I) of plants fumigated with 800 \mu g SO₂ m^{-3} and of control plants are given in Table 3. The parameter values of the control plants did not change during the 2-h period. At low concentrations of \CO₂ the \CO₂ assimilation rate was reduced by fumigation with SO₂, but at high \CO₂ concentrations no effect of SO₂ fumigation could be detected (Fig. 5). Both the estimated \CO₂ compensation point and the mesophyll resistance to \CO₂ increased as a result of SO₂ exposure (Table 3). The lack of inhibition of \CO₂ assimilation by SO₂ at high \CO₂ concentrations was also reported by Carlson (1983) for

![Figure 4. Rates of \CO₂ assimilation after a 2-h fumigation period relative to control rates before fumigation in relation to SO₂ uptake rates (\mu g SO₂ m^{-2} s^{-1}). Pₚ \%(of control) = 100-23.19\times F (r^2 = 0.55, \text{n} = 20).](image)

![Figure 5. Net \CO₂ assimilation rate of Vicia faba leaves in relation to calculated internal \CO₂ concentration (\text{C}_i) before (\text{B}), and after 2-h (\text{B'}) fumigation with 800 \mu g m^{-3} fitted with eqn (2). Dotted lines represent the \CO₂ supply functions before (\text{B}) and after fumigation (\text{B'}) of plants measured at an ambient \CO₂ concentration of 340 ppm \CO₂ (average values of five plants). The measured time course of the change in \CO₂ assimilation and \text{C}_i of these plants is enlarged in the inset. The numbers give time in minutes after the start of fumigation.](image)

### Table 2. Ratio of rates of photosynthesis and transpiration (P/T)

<table>
<thead>
<tr>
<th>n</th>
<th>\text{SO₂} (\mu g m^{-3})</th>
<th>Before</th>
<th>After</th>
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<tr>
<td>4</td>
<td>100</td>
<td>7.37±0.79</td>
<td>7.05±0.70</td>
</tr>
<tr>
<td>4</td>
<td>200</td>
<td>8.97±0.47</td>
<td>8.48±0.56</td>
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<tr>
<td>14</td>
<td>400</td>
<td>9.88±0.37</td>
<td>8.94±0.27</td>
</tr>
<tr>
<td>6</td>
<td>800</td>
<td>9.02±1.01</td>
<td>8.06±1.44</td>
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soybean leaves. Black (1982) demonstrated that the suppression of the effects of SO$_2$ at high CO$_2$ concentrations was not caused by stomatal closure due to enhanced CO$_2$ concentrations.

The role of stomatal resistance in the observed reduction of the rate of CO$_2$ uptake was analysed by plotting the time course of net leaf photosynthesis versus $C_t$ at an ambient CO$_2$ concentration of 340 ppm (Fig. 5 inset). A strong reduction in net photosynthesis occurred during the first 10 min of fumigation, with a trajectory that closely followed the CO$_2$-supply function (dotted lines), indicating that the reduction was entirely due to an increasing mesophyll resistance. An increase in stomatal resistance occurred later, as can be observed by following the trajectory of the photosynthesis-$C_t$ curve in time. These results suggest that SO$_2$ induces an increase in mesophyll resistance which results in lowered photosynthetic rates. Stomata close later as a result of a feedback loop between net photosynthesis, internal CO$_2$ concentration and stomatal resistance. The constant ratio between internal CO$_2$ concentration and ambient CO$_2$ concentration both before and after fumigation (Table 4) support the conclusion that stomatal behaviour is not influenced by SO$_2$. Further analysis of Carlson’s (1983) data showed that SO$_2$ did not affect the $C_i/C_a$ ratio in soybeans either, supporting the conclusion that stomatal behaviour is not altered by SO$_2$.

Several workers also found stomatal closure in plants of Vicia faba and other species exposed to low concentrations of SO$_2$ at low relative humidity, but stomatal opening at high relative humidity (Majernik & Mansfield, 1971; Black & Unsworth, 1980). Black & Unsworth (1980) observed stomatal opening at both low and high relative humidity in Phaseolus vulgaris, while Temple, Fa & Taylor (1985) observed stomatal closure in this species. Other workers reported no change or a slight reduction in stomatal conductance (Barton et al., 1980) at low concentrations of SO$_2$ or reductions in stomatal conductance (i.e. Müller, Miller & Sprügel, 1979; Olszyk & Tibbits, 1981). The contradictory results of many studies were discussed by Black (1982) and Mansfield & Freer-Smith (1984). The mechanism behind stomatal opening in response to SO$_2$ was analysed by Black & Black (1979) who observed damage in the epidermal cells of Vicia faba leaves surrounding the intact guard cells. Stomatal responses to light were unchanged. A possible explanation for the absence of such an effect in other studies could be a different physiological status of the plants used. In most studies, the effect of SO$_2$ on stomatal behaviour and photosynthesis are analysed separately. The method of analysis presented in this paper may help to obtain more insight into the interaction between various physiological reactions of plants during exposure to air pollutants.

From in vivo gas exchange measurements it appears that the effects of SO$_2$ are reversible and suppressed at high CO$_2$ concentrations (Fig. 5, Black, 1982; Carlson, 1983), which supports the competitive mechanism of SO$_2$ inhibition suggested by Ziegler (1975). From Table 3 it appears that both the CO$_2$ compensation point and the mesophyll resistance increased after SO$_2$ fumigation. An increase in the CO$_2$ compensation point was also reported by Furukawa, Natori & Totsuka (1980) and Jensen & Noble (1984). This increase in $C_i$ indicates that the effect of SO$_2$ on CO$_2$ assimilation cannot be explained by an equal competitive effect of sulphur metabolites with respect to CO$_2$ and O$_2$. The observed increase in the CO$_2$ compensation point and mesophyll resistance can only be explained by a stronger effect of sulphur compounds on the affinity of the enzyme for CO$_2$ ($K_c$) than on its affinity for O$_2$ ($K_o$). These effects can be quantified in gas exchange measurements at a range of CO$_2$ concentrations at both normal and low oxygen concentrations to...
separate $SO_2$ effects on carboxylation and oxygenation of RBP carboxylase/oxygenase.

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References


