

Absorption of SO₂ by Pecan (*Carya illinoensis* (Wang) K. Koch) and Alfalfa (*Medicago sativa* L.) and its Effect on Net Photosynthesis¹

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ABSTRACT

Absorption rates of SO₂ by pecan (*Carya illinoensis* (Wang) K. Koch) leaflets exposed to 2.6, 5.2, and 7.8 mg SO₂ m⁻³ were measured over a 2 h period. SO₂ was rapidly absorbed by the leaflets in all treatments during the initial 30–50 min; the rate of uptake decreased to a rather constant level thereafter. Total SO₂ absorbed during the 2 h period was 15.6, 25.6, and 38.9 nmol cm⁻² for the low, medium, and high SO₂ concentrations, respectively. Reductions in net photosynthetic rates were proportional to ambient SO₂ concentrations and total SO₂ absorbed. Partial photosynthetic recovery occurred in all treatments during a 2 h post-treatment period and full recovery occurred during a 12 h dark period. Exposure to SO₂ resulted in slight increases in stomatal and boundary layer resistances to CO₂ and substantial increases in residual resistances. Absorption rates of SO₂ by alfalfa (*Medicago sativa* L.) exposed to 5.2 mg SO₂ m⁻³ for 1 h were approximately double those of pecan exposed to the same ambient SO₂ concentration. Alfalfa net photosynthetic rates were reduced 74% after 1 h exposure to 5.2 mg SO₂ m⁻³ while a depression of 42% occurred in pecan.

INTRODUCTION

The concern with SO₂ as an atmospheric pollutant is well publicized. Sulphur is an essential mineral for plants and exposure to low concentrations could be beneficial rather than detrimental. This is especially true if plants have a limited supply of sulphur and sulphur deficiencies exist (Cowling, Jones, and Lockyer, 1973; Thomas, Hendricks, Collier, and Hill, 1943). However, acute and chronic exposure to SO₂ at concentrations equal to or above those measured near industrial sources have resulted in predominantly deleterious effects. Sulphur dioxide has been shown to reduce plant growth, with or without visible injury (Karnosky, 1976; Heck and Brandt, 1977), induce leaf necrosis (Bressan, Wilson, and Filner, 1978), and inhibit several processes of plant metabolism (reviewed by Ziegler, 1975).

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Inhibition of plant photosynthesis by SO₂ has been shown for a number of species (Bennet and Hill, 1973; Slack and Unsworth, 1979; Sij and Swanson, 1974). The ability of SO₂-affected photosynthetic rates to recover to pretreatment rates in SO₂-free air is well documented in these and other studies. Specific effects on photosynthesis that have been demonstrated are inhibition of cyclic and non-cyclic photophosphorylation (Silvius, Ingle, and Baer, 1975) and of carboxylase activity (Ziegler, 1975), destruction of chlorophyll (Malhotra, 1977), and loss of chloroplast membrane integrity (Wellburn, Majernik, and Wellburn, 1972).

A nearly linear relationship between several ambient SO₂ concentrations and net photosynthetic inhibition has been reported by Bennett and Hill (1973), and at the lower SO₂ concentrations tested by Black and Unsworth (1979). However, it is not apparent whether this relationship corresponds to the total SO₂ absorbed during the exposure period. Thus, the objectives of the present study were (1) to determine if photosynthetic responses of pecan (*Carya illinoensis* (Wang) K. Koch) leaflets exposed to four concentrations of SO₂ (1.3, 2.6, 5.2, and 7.8 mg SO₂ m⁻³) were related to ambient SO₂ concentration, (2) to determine the absorption rates and relative photosynthetic sensitivities of pecan leaflets and alfalfa (*Medicago sativa* L.) to SO₂ exposure, and (3) to determine if the total SO₂ absorbed by pecan leaflets exposed to three ambient SO₂ concentrations during a 2 h exposure period was linearly related to photosynthetic inhibition.

MATERIALS AND METHODS

Grafted pecan (*Carya illinoensis* (Wang) K. Koch) 'Wichita' trees, maintained for 3 years in 115 l metal barrels were utilized in these experiments. The Wichita cultivar was selected because it had been observed to be more sensitive to SO₂ than other cultivars tested. The trees had trunk diameters of 2.5–3.7 cm. The growth medium was a 1:1 mixture of sphagnum peat and Perlite. Mineral nutrition was provided by weekly watering with Peters² 10-10-10 solution plus Standard Trace Element Solution (STEM) during the growing season. Additional iron, zinc, and manganese was supplied in bi-weekly foliar sprays of a solution containing 9 g each of FeSO₄·7H₂O, ZnSO₄·7H₂O, and MnSO₄·H₂O per 3.8 l H₂O. Insect control was employed as needed using Disulfaton systemic insecticide. Alfalfa (*Medicago sativa* L.) 'Mesilla' plants were grown in 12 cm pots using a 1:1 mixture of Jiffy-Plus and Perlite. Fertilization of alfalfa plants was the same as described above for pecan except foliar sprays containing iron, zinc, and manganese were not used. The plants were grown in a greenhouse and were approximately 3 months old when the experiments were initiated.

Net photosynthetic rates were determined for the terminal leaflet of intact pecan leaves with an open gas circulation system incorporating a Beckman Model 865 IR gas analyser. Air and leaf temperatures within the gas exchange cuvette were measured with fine-wire (copper-constantan) thermocouples. Photosynthetically active photon flux density (PAR; 400–700 nm) was monitored with a Lambda Instruments Corp. Model LI-190SR quantum sensor. Flow rates of air through the Plexiglass cuvette (0.2 l volume) were constantly monitored by two flowmeters and maintained at 1 or 2 l min⁻¹, depending on leaf size. One 1500 W Westinghouse tungsten-halogen lamp provided a photon flux density of 850 μE m⁻² s⁻¹ PAR for all photosynthetic determinations. Fluctuations in water vapour concentrations occurring within the cuvette were measured with two Cambridge Model 880 dewpoint hygrometers. Leaf diffusive resistances to CO₂ were calculated by the methods outlined by Sisson and Caldwell (1976). Photosynthetic rates are expressed on a leaf area (one side) basis. Leaf areas were measured with a Lambda Instruments Corp. Model LI-3000 portable area meter. Air temperatures within the cuvette were maintained at 27 ± 1 °C with relative humidities of greater than 60% during all photosynthetic rate determinations.

² The use of trade names does not constitute an official endorsement or approval by the U.S. Department of Agriculture.

Photosynthetic rates of selected terminal pecan leaflets were determined during an equilibration period prior to SO₂ exposure. Leaflets that displayed photosynthetic rates which varied more than 10% from the initial leaflet used in any experiment during the equilibration period were replaced with leaflets of more comparable activity.

Specific concentrations of SO₂ were maintained inside a greenhouse situated 39 m³ fumigation chamber covered with clear acetate plastic as described previously by Booth, Throneberry, and Lujan (1976). Sulphur dioxide (anhydrous 99.98% purity, Matheson Chemical Co.) was introduced into the chamber through the intake airstream and distributed in the chamber through perforated floor ducts. The SO₂ flow rate was metered by a microvalve and flowmeter. A 425 m³ min⁻¹ roof-mounted exhaust fan maintained continuous air movement through the chamber and served to diffuse the SO₂ within the chamber. Air within the chamber was continuously monitored for SO₂ during the experimental periods with a Thermo Electron Corp. Series 43 pulsed fluorescent SO₂ analyser. A Model 8500 Monitor Labs Inc. calibrator was used to calibrate the SO₂ analyser prior to each fumigation period. The instruments used for measuring SO₂ and calibrating the SO₂ analyser were maintained in a temperature-controlled (24-26°C) instrument trailer immediately adjacent to the greenhouse that contained the two chambers. An identical second chamber was used as a source of SO₂-free air during the pre- and postfumigation periods.

Terminal leaflets of pecan leaves were exposed to four SO₂ concentrations (1.3, 2.6, 5.2, and 7.8 mg SO₂ m⁻³). After equilibrium photosynthetic rates were achieved within the gas-exchange cuvette with SO₂-free air, air containing the specific concentration of SO₂ being tested was pumped from the fumigation chamber to the gas-exchange cuvette through Teflon tubing. Prior to CO₂ analysis, the air was dried in a magnesium perchlorate column which also removed most of the SO₂. Absorption of SO₂ was measured as the difference in SO₂ concentration of the gas-exchange cuvette incoming and outgoing airstreams. Absorption of SO₂ by the gas-exchange cuvette was determined during two 1 h periods. There was no measurable absorption of SO₂ by the cuvette in the absence of leaves. Deposition velocities were calculated by the formula:

$$\text{Deposition velocity} = \frac{\mu\text{g SO}_2 \text{ absorbed cm}^{-2} \text{ s}^{-1}}{\mu\text{g SO}_2 \text{ cm}^{-3} \text{ air}} \quad (1)$$

described by Spedding (1969). The SO₂ concentration of the air-stream into the cuvette comprised the $\mu\text{g SO}_2 \text{ cm}^{-3}$ air in these calculations.

RESULTS

The absorption of SO₂ by the terminal leaflet of pecan leaves and its effect on net photosynthesis are depicted in Fig. 1A, B, and C. Net photosynthetic rates of leaflets exposed to 7.8 mg SO₂ m⁻³ for 2 h were reduced by 68% from the prefumigation equilibrium rate (Fig. 1A). Leaflets exposed to 5.2 (Fig. 1B) and 2.6 (Fig. 1C) mg SO₂ m⁻³ were reduced by 54 and 28%, respectively. The photosynthetic rates of leaflets exposed to 1.3 mg SO₂ m⁻³ were reduced from 10.9 mg CO₂ dm⁻² h⁻¹ (± 0.36 s.d.) during the prefumigation period to 9.6 mg CO₂ dm⁻² h⁻¹ (± 0.58 s.d.) at the end of the 2 h fumigation periods (12% reduction). Thus, a linear ($r^2 = 0.97$) relationship exists between percent reductions in photosynthesis during 2 h exposures to SO₂ and the four SO₂ concentrations tested.

Reductions in net photosynthesis occurred primarily during the first hour of SO₂ exposure, with limited reductions occurring thereafter. Exposures to 5.2 mg SO₂ m⁻³ resulted in a mean increase in net photosynthesis after 1 h of treatment (Fig. 1B). However, this increase was not significantly ($P < 0.05$) greater than any rate determined after 30 min exposure to SO₂.

Sulphur dioxide was rapidly absorbed by leaflets during the initial 30-50 min of treatment, followed by rather constant uptake phases thereafter (cf. Fig. 1A, B, and C). Diffusion of SO₂ into stomatal cavities was not measured separately from that

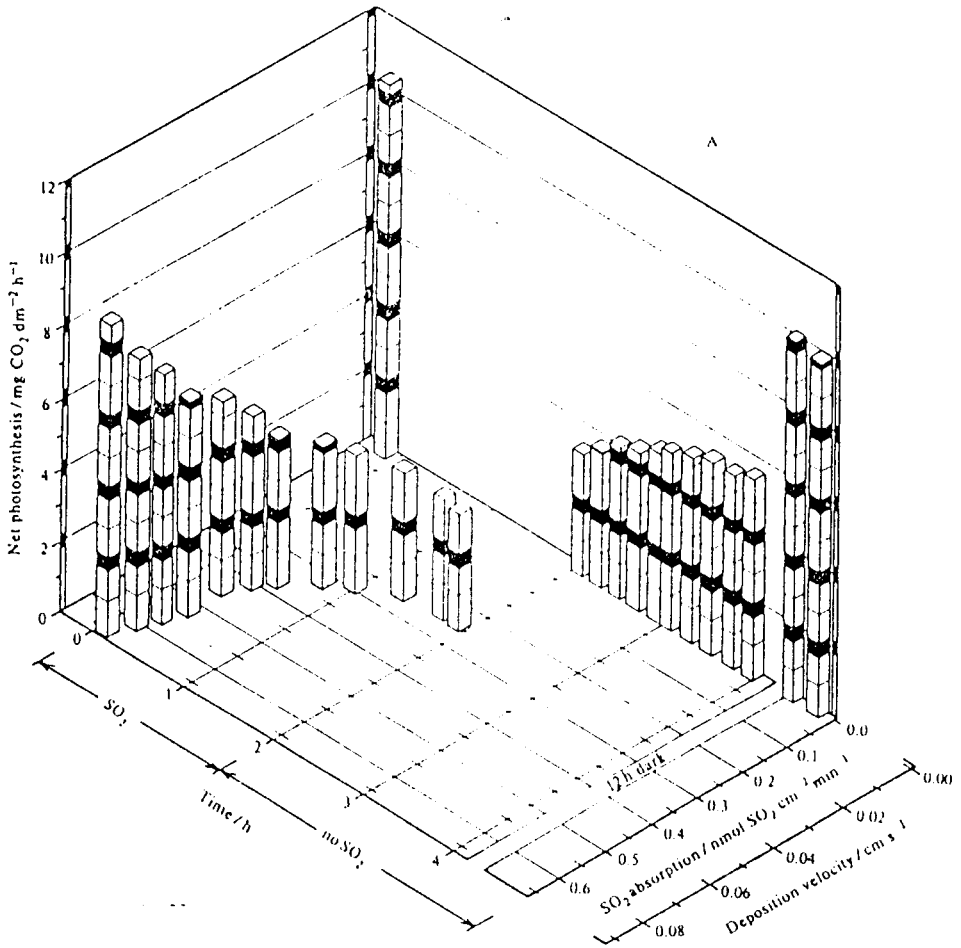
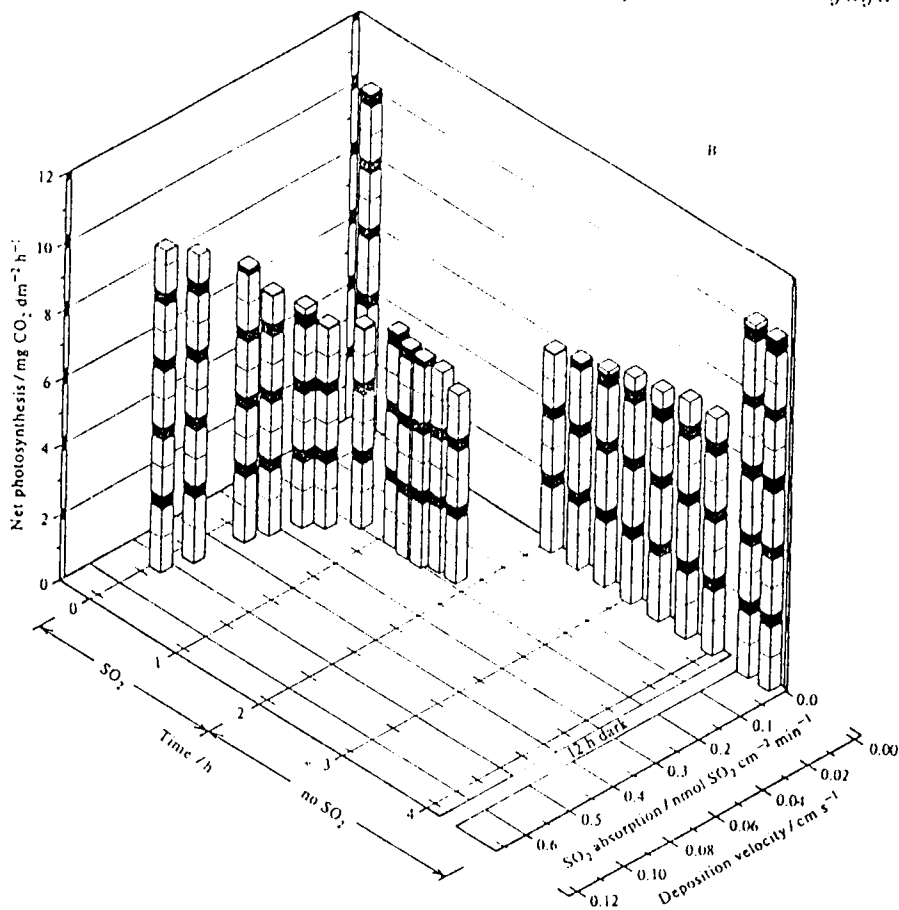


FIG. 1 Net photosynthesis, SO_2 absorption, and SO_2 deposition velocities of the terminal leaflet of pecan (*Carya illinoensis* (Wang) K. Koch) leaves during 2 h exposure to (A) $7.8 \text{ mg SO}_2 \text{ m}^{-3}$, (B) $5.2 \text{ mg SO}_2 \text{ m}^{-3}$, and (C) $2.6 \text{ mg SO}_2 \text{ m}^{-3}$ and a 2 h post treatment period in SO_2 -free air. Each value represents the mean of 3–6 replicates. Standard errors ranged from 0.21 to 1.01 for the photosynthetic rates, 0.01 ($2.6 \text{ mg SO}_2 \text{ m}^{-3}$ treatment) to 0.09 ($7.8 \text{ mg SO}_2 \text{ m}^{-3}$ treatment) for the SO_2 absorption rates, and 0.004 ($2.6 \text{ mg SO}_2 \text{ m}^{-3}$ treatment) to 0.012 ($7.8 \text{ mg SO}_2 \text{ m}^{-3}$ treatment) for the deposition velocities. PAR irradiance (400–700 nm) was $850 \mu\text{E m}^{-2} \text{ s}^{-1}$ with air temperature maintained at $27 \pm 1^\circ\text{C}$.

absorbed onto the leaflet surface. Thus, the absorption rates reflect both phenomena.

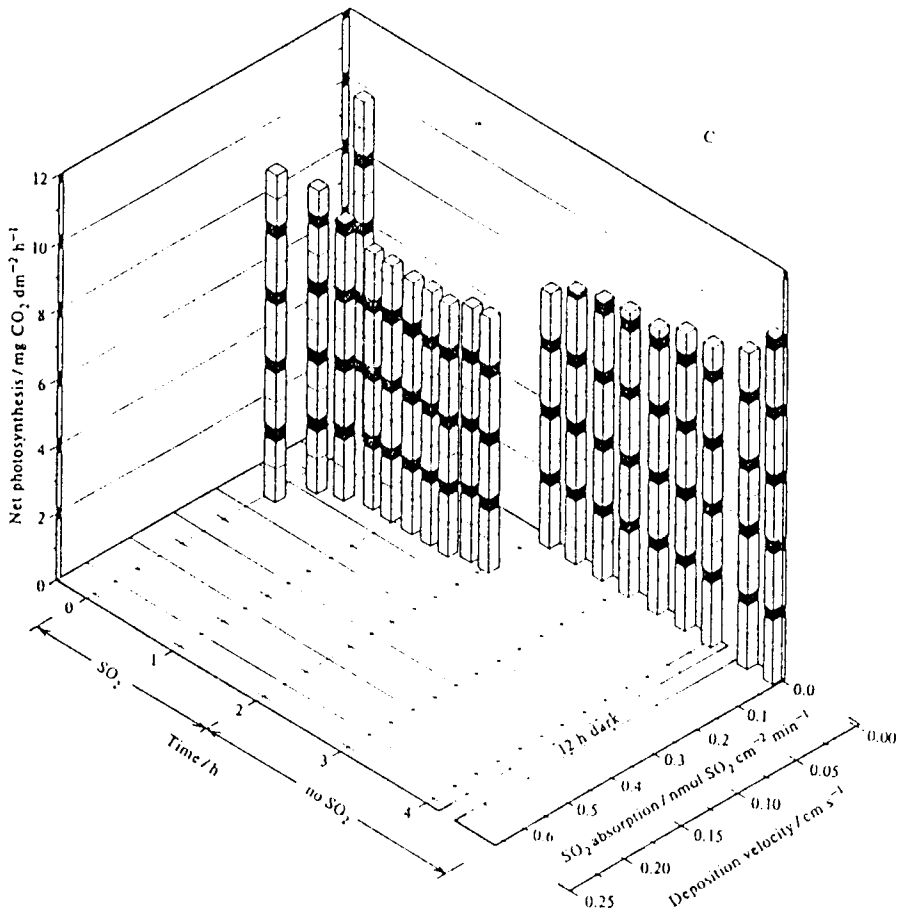
Mean amounts of SO_2 absorbed by the leaflets during the 2 h exposure periods were 15.6, 25.6, and 38.9 nmol $\text{SO}_2 \text{ cm}^{-2}$ for the 2.6, 5.2, and $7.8 \text{ mg SO}_2 \text{ m}^{-3}$ treatments, respectively. Total SO_2 absorption was proportional to the ambient concentration. Thus, the reductions in net photosynthesis that occurred during the 2 h exposures were related to the SO_2 concentration as noted above, and were proportional to the total SO_2 absorbed. A dependence of net photosynthetic rate inhibition on ambient SO_2 concentration was similarly observed for *Vicia faba* L. by Black and Unsworth (1979) at lower concentrations ($<0.3 \text{ mg SO}_2 \text{ m}^{-3}$).



Deposition velocities over the 2 h treatment period are shown in Fig. 1A, B, and C for pecan leaflets. These values were similar at all three SO₂ concentrations tested when compared at equal times during the 2 h treatment period. Maximum deposition velocities of approximately 0.090 cm s⁻¹ occurred during the initial 30 min of the fumigation period with a somewhat constant rate of about 0.035 cm s⁻¹ during the last 30 min of the treatment periods.

During the 2 h postfumigation period, partial recovery of net photosynthetic rates occurred in pecan leaflets exposed to all three SO₂ concentrations (Fig. 1A, B, and C.). Full recovery to the prefumigation rates occurred for all SO₂ concentrations tested only after a 12 h dark period. Although the mean net photosynthetic rates achieved after the 12 h dark period were somewhat higher than those measured during the prefumigation period, no significant statistical differences ($P < 0.05$) were found.

No visible injury occurred in the leaflets exposed for 2 h to 1.3, 2.6, or 5.2 mg SO₂ m⁻³ during the course of the experiment or during a 2 week period after the SO₂ treatments. However, the 7.8 mg SO₂ m⁻³ treatment concentration resulted in slight chlorosis of abaxial intervenal tissue of three of six leaflets tested. This



bleaching appeared during the first week after treatment and affected less than 5% of the total leaf surfaces.

Net photosynthetic rates of pecan leaflets were also determined during a 30 min exposure period to the same SO₂ concentrations used in the previous experiments. These experiments were conducted to determine if a shorter exposure period would result in greater recovery in net photosynthetic rates during the 2 h postfumigation period than occurred following the 2 h exposures. Reductions in photosynthesis during the 30 min SO₂ treatment period were comparable to those which occurred during the initial 30 min of the 2 h fumigations (Fig. 1A, B, and C). Complete recovery to the prefumigation photosynthetic rates during the 2 h post-treatment period occurred only in leaflets exposed to 2.6 mg SO₂ m⁻³ for 30 min. Leaflets exposed to 5.2 and 7.8 mg SO₂ m⁻³ recovered to within approximately 85% of the prefumigation photosynthetic rate before recovery ceased. These results closely agree with those of Sij and Swanson (1974) in which bean (*Phaseolus vulgaris* L.) exposed to 2.6 mg SO₂ m⁻³ for 1 h recovered to prefumigation photosynthetic rates after approximately 30 min in SO₂-free air. They also showed that exposure of bean to 7.8 mg SO₂ m⁻³ for 1 h resulted in a recovery to within 75–90% of the

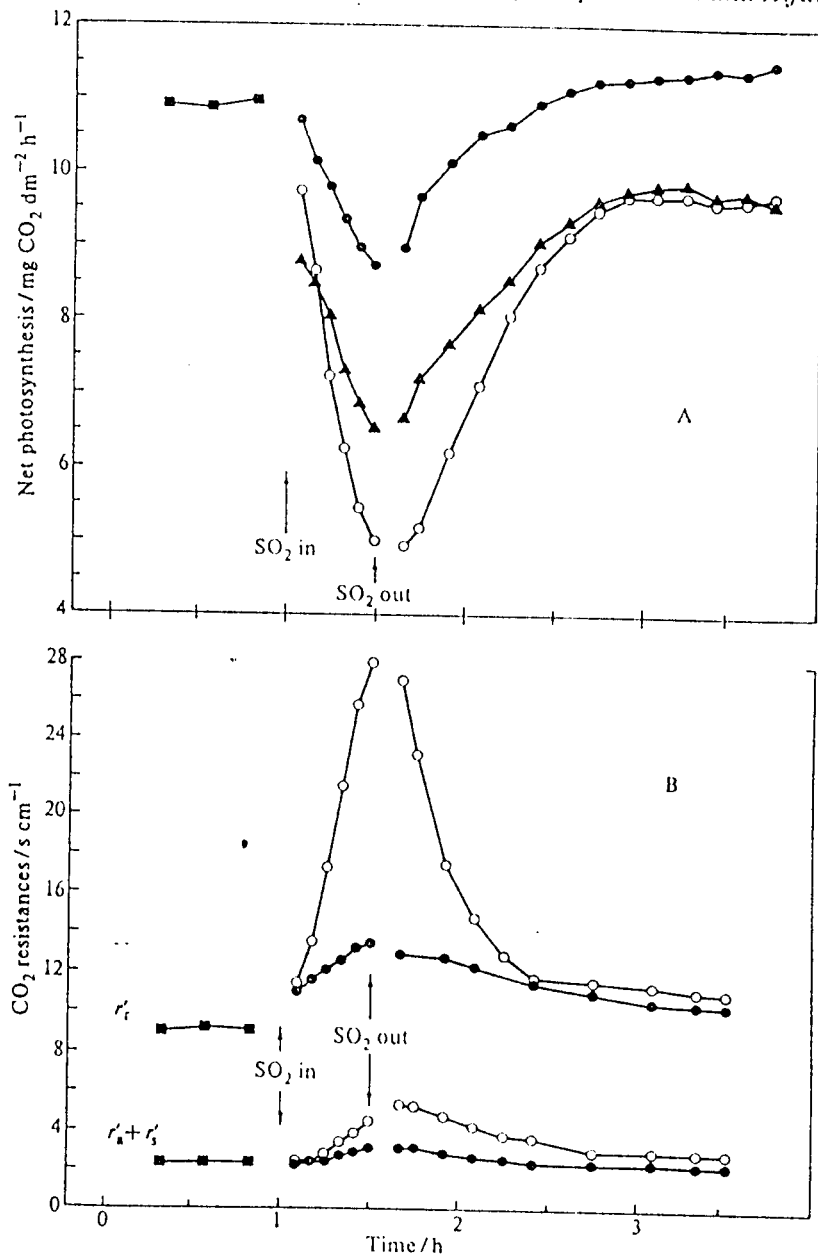


FIG. 2. Net photosynthesis (Δ) and CO_2 resistances (r_t' : residual resistance, $r_a' + r_s'$: leaf resistances) (\square) of the terminal leaflet of pecan (*Carya illinoensis* (Wang) K. Koch) leaves during 30 min exposure to 2.6 $\text{mg SO}_2 \text{ m}^{-3}$ (\bullet — \bullet), 5.2 $\text{mg SO}_2 \text{ m}^{-3}$ (\blacktriangle — \blacktriangle), and 7.8 $\text{mg SO}_2 \text{ m}^{-3}$ (\circ — \circ) and a 2 h post-treatment period in SO_2 -free air. Each value represents the mean of three or four replicates. Standard errors ranged from 0.81 to 1.21 for photosynthesis, 0.17 to 0.68 for $r_a' + r_s'$ and 0.19 to 2.43 for r_t' . PAR irradiance (400-700 nm) was $850 \mu\text{E m}^{-2} \text{ s}^{-1}$ with air temperature maintained at $27 \pm 1^\circ\text{C}$.

prefumigation rates during the postfumigation period. The degree of recovery was also shown to be dependent upon leaf age.

The calculated leaf ($r_a' + r_s'$) and residual (r_t') CO_2 resistances for leaflets during

the 30 min treatment and 2 h post treatment period are shown in Fig. 2b. The resistances associated with leaflets treated with 5.2 mg SO₂ m⁻³ were intermediate to those determined for the 2.6 and 7.8 mg SO₂ m⁻³ treatments with maximum mean values of 22.4 and 3.8 for the r'_t and $r'_a + r'_s$, respectively. The mean $r'_a + r'_s$ of the leaflets exposed to 2.6 mg SO₂ m⁻³ did not increase until after 15 min of the 30 min treatment period with only a slight increase occurring thereafter. This degree of increase in $r'_a + r'_s$ indicates that stomatal closure was not impairing movement of CO₂ or SO₂ into the stomatal cavity. A more substantial increase in $r'_a + r'_s$ occurred in leaflets exposed to 7.8 mg SO₂ m⁻³, suggesting that stomatal aperture was affected and may have somewhat restricted movement of both SO₂ and CO₂ during the latter phase of the 30 min exposure period. However, the large increase in r'_t that occurred in both treatments (Fig. 2b) suggests that this resistance to CO₂ movement was primarily responsible for depressions in photosynthesis rather than those resistances associated with stomatal aperture ($r'_a + r'_s$). Exposure of leaflets to SO₂-free air during the 2 h postfumigation period resulted in rapid reductions in both r'_t and $r'_a + r'_s$. There were no significant statistical differences ($P < 0.05$) between prefumigation resistances (r'_t and $r'_a + r'_s$) and resistances determined at the end of the postfumigation period. However, the mean r'_t at the end of the postfumigation period was higher in all three SO₂ treatments than during the prefumigation period.

Absorption of SO₂ by alfalfa exposed to 5.2 mg SO₂ m⁻³ for 1 h and the resultant effects on photosynthesis are shown in Fig. 3. Photosynthesis was reduced from a prefumigation rate of 19.2 mg CO₂ dm⁻² h⁻¹ to 4.9 mg CO₂ dm⁻² h⁻¹ at the end of the fumigation period. This reduction occurred primarily during the initial 30 min of the 1 h exposure period as occurred in pecan (Fig. 1A, B, and C). The calculated resistances indicate that CO₂ resistances associated with stomatal and boundary layers ($r'_a + r'_s$) were only slightly, and not significantly ($P < 0.05$), affected. An increase in $r'_a + r'_s$ from 3.03 s cm⁻¹ to 4.55 s cm⁻¹ occurred during the treatment period. However, the resistances associated with the liquid phase and biochemical reactions of CO₂ (r'_l) substantially increased through the exposure period, similar to the r'_t increase calculated for pecan; an increase from 5.40 (± 0.5 s.d.) to 25.60 (± 2.6 s.d.) s cm⁻¹ occurred during the 1 h fumigation. The apparent lack of stomatal closure indicated by the $r'_a + r'_s$ values is reflected in the high rates of SO₂ absorption that occurred throughout the treatment period. Sulphur dioxide was absorbed at a rate of 0.76 nmol SO₂ cm⁻² min⁻¹ after 10 min exposure to SO₂, and 0.44 nmol SO₂ cm⁻² min⁻¹ after 1 h. These rates of absorption were nearly double those of pecan exposed to the same concentration of SO₂ (5.2 mg SO₂ m⁻³) after 10 min and approximately triple that of pecan after 1 h. Pecan leaflet photosynthetic rates were reduced by 42% after 1 h exposure, while a depression of 74% occurred in alfalfa.

The deposition velocities shown in Fig. 3 for alfalfa are considerably higher than those calculated for pecan leaflets. After 5 min exposure to 5.2 mg SO₂ m⁻³, the deposition velocities for pecan and alfalfa were 0.094 and 0.158 cm s⁻¹, respectively. At the termination of the 30 min SO₂ treatment period, the comparable value for alfalfa was reduced by 43% to 0.089 cm s⁻¹.

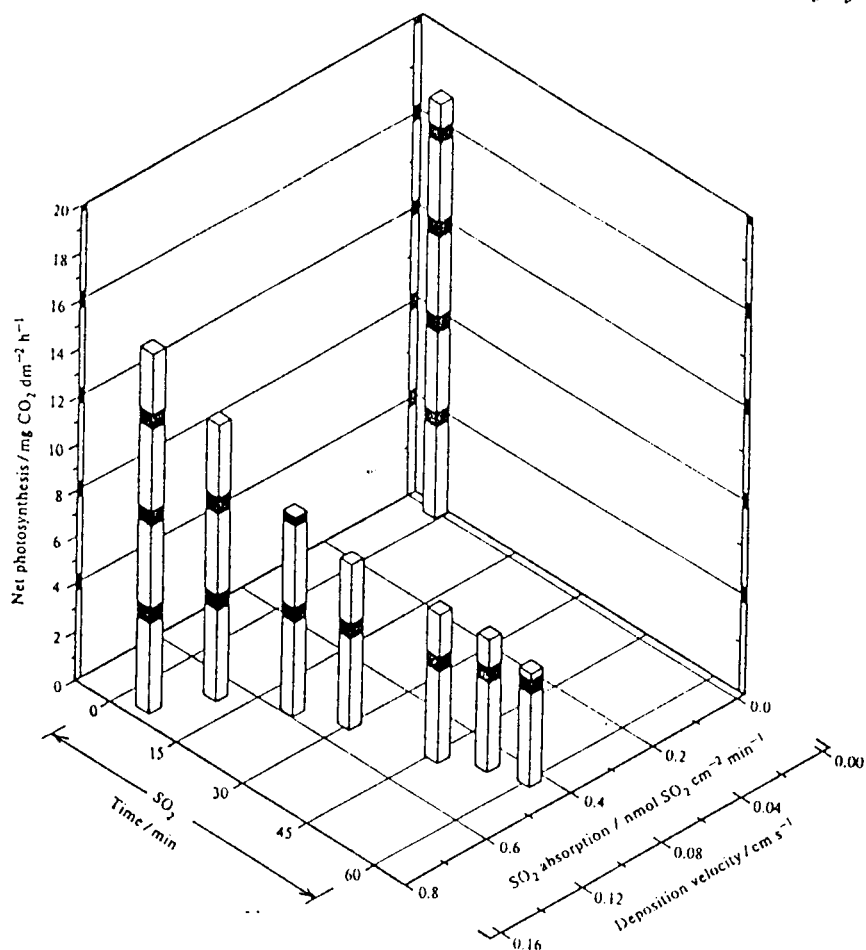


FIG. 3. Net photosynthesis, SO_2 absorption, and SO_2 deposition velocities for alfalfa (*Medicago sativa* L.) exposed to $5.2 \text{ mg SO}_2 \text{ m}^{-3}$ for 60 min. Each value represents the mean of three replicates. Standard errors ranged from 0.82 to 2.11 for photosynthesis, 0.09 to 0.16 for SO_2 absorption, and 0.006 to 0.017 for the deposition velocities. PAR irradiance (400–700 nm) was $850 \mu\text{E m}^{-2} \text{ s}^{-1}$ with air temperature maintained at $27 \pm 1^\circ\text{C}$.

DISCUSSION

Exposure of the terminal leaflet of pecan leaves to 1.3, 2.6, 5.2, and $7.8 \text{ mg SO}_2 \text{ m}^{-3}$ resulted in almost immediate reductions in net photosynthesis. The suppressions of net photosynthesis at the end of 2 h exposure periods were proportional to ambient SO_2 concentrations, SO_2 absorption rates, and total SO_2 absorbed per unit leaf area. Other studies using barley (*Hordeum vulgare* L.), alfalfa, and *Vicia faba* showed a similar type of dependence of photosynthetic inhibition on ambient SO_2 concentration (Bennett and Hill, 1973; Black and Unsworth, 1979). A curvilinear inhibition in net photosynthesis with increasing SO_2 concentrations occurred in *V. faba* with light saturation. In the present study, the comparatively higher SO_2 concentrations tested were still not high enough to cause an apparent saturating effect on photosynthetic inhibition in pecan.

Bressan *et al.* (1978) found that SO_2 absorption rates were the primary factor

determining the relative sensitivity of several cultivars of the Cucurbitaceae. They indicated that their data supported the hypothesis of Thomas (1961) that differential sensitivities of plant species to SO₂ result from absorption rate differences. The absorption rates for pecan were approximately 40% lower than for alfalfa at equivalent ambient SO₂ concentration (5.2 mg SO₂ m⁻³) and exposure period (60 min) (Figs 2B and 3). During this 60 min exposure period, net photosynthetic rates were reduced by 74% from the prefumigation equilibrium rates in alfalfa and by 42% in pecan. Although no leaf damage occurred in the present experiments with alfalfa, it has been shown to be extremely sensitive to SO₂-induced leaf damage, whereas pecan is somewhat resistant (Booth *et al.*, 1976). Thus, the hypothesis forwarded by Thomas (1961) tends to be supported by the results of the present study if only absorption rates or deposition velocities are considered. However, differential metabolically-based sensitivities to SO₂ may also have to be considered. For example, Ziegler (1975) indicates that PEP carboxylase of C₄ plants is relatively sulfite-insensitive, whereas RuBP carboxylase of C₃ plants is very sensitive to sulfite. Vogl and Börtitz (1965) found that differential sensitivities of species within *Larix* and *Picea* genera were due to plasmatic factors. In addition, immature leaves have been found to be more resistant to SO₂ than mature leaves (Stratmann, 1963) while displaying similar SO₂ absorption rates (Bressan *et al.*, 1978). Bressan *et al.* (1978) suggest that young leaves possess some type of metabolically-based resistance to SO₂ that is developmentally controlled. Thus, a simple cause (i.e. absorption rate) and effect (e.g. leaf damage, photosynthetic inhibition) relationship with regard to plant reaction to SO₂ may be somewhat tenuous.

Alfalfa absorbed SO₂ at a rate nearly double that of pecan when exposed to 5.2 mg SO₂ m⁻³ for 1 h (Figs 1B and 3). This large differential in SO₂ absorption rates was not related to stomatal number. Alfalfa possesses about 17 000 and 19 000 stomata cm⁻² on the abaxial and adaxial leaf surfaces, respectively (Meidner and Mansfield, 1968). Pecan leaflets have approximately 48 000 stomata cm⁻² only on the abaxial leaf surface. This lack of correlation between absorption rates, stomatal frequency, and plant species sensitivity has also been shown by Bressan *et al.* (1978) and Zimmerman and Hitchcock (1956).

Several investigators have demonstrated for a number of species that exposure to SO₂ results in stimulating both stomatal opening (Majernik and Mansfield, 1970, 1971; Unsworth, Biscoe, and Pinckney, 1972) and closure (Sij and Swanson, 1974). Leaf resistances ($r'_a + r'_s$) of pecan (Fig. 2B) and alfalfa increased upon exposure to all SO₂ concentrations tested. The degree of increase in $r'_a + r'_s$ appeared to be somewhat dependent upon the ambient SO₂ concentration for pecan (Fig. 2B). The $r'_a + r'_s$ increased in leaflets exposed to 2.6 mg SO₂ m⁻³ from a prefumigation value of 2.3 to a value of 3.1 s cm⁻¹ after 30 min treatment; an increase to 4.5 s cm⁻¹ occurred after 30 min exposure to 7.8 mg SO₂ m⁻³. The $r'_a + r'_s$ of the leaflets exposed to 7.8 mg SO₂ m⁻³ continued to increase after termination of SO₂ treatment and introduction of SO₂-free air. This increase is not thought to have resulted from residual SO₂ in the cuvette during the postfumigation period since the air flow rates exchanged the air within the cuvette approximately 5

times per minute. Instead, the increase probably resulted because of the time lag involved between SO₂ absorption and its movement to the site of influencing stomatal aperture.

Substantial increases in residual resistances (r'_t) occurred during exposure of pecan leaflets (Fig. 2B) and alfalfa to SO₂. Several component reactions of photosynthesis have been shown to be adversely affected by exposure to SO₂ and these effects would be reflected in the increases in r'_t determined in the present study. Among others, SO₂ inhibits cyclic and non-cyclic photophosphorylation (Silvius *et al.*, 1975), is a competitive inhibitor of bicarbonate attachment to RuBP carboxylase (Ziegler, 1972) and disrupts chloroplast membrane ultrastructure (Wellburn *et al.*, 1972). Net photosynthetic rates of pecan leaflets exposed to the three highest SO₂ concentrations for 2 h recovered to prefumigation rates after a 12 h dark period. Pecan leaflets exposed to 30 min of 2.6 mg SO₂ m⁻³ recovered to prefumigation rates during a 2 h postfumigation period. Thus, the effect of SO₂ on the photosynthetic apparatus appeared to be temporary. However, these results do not preclude the possibility that more permanent damage to the photosynthetic apparatus occurred.

Results of the present study indicate that ambient SO₂ concentrations within the range of 1.3–7.8 mg SO₂ m⁻³ have an immediate but temporary inhibiting effect on the photosynthetic process of pecan leaflets. However, caution should be exercised in attempting to extrapolate results from this study to plant responses in field situations. In the present study, an attempt was made to eliminate plant stress by providing adequate nutrient and water levels. Furthermore, SO₂ concentrations were precisely maintained during the fumigation periods, leaf boundary resistances were minimized by high air flow rates, and pecan leaflets were held at normal incidence to a light source that emitted a constant PAR level. Such constancy of these factors would not exist simultaneously, or for the duration maintained during this study for even a portion of the leaves comprising a plant canopy in a field situation. The interactive effect of constantly fluctuating SO₂ concentrations and environmental factors in a field situation considerably reduces the ability to make accurate predictions of plant responses to SO₂ in the field.

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