Stomatal Conductance and Sulfur Uptake of Five Clones of *Populus tremuloides* Exposed to Sulfur Dioxide

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ABSTRACT

Plants of five clones of *Populus tremuloides* Michx. were exposed to 0, 0.2 or 0.5 microliter per liter SO₂ for 8 hours in controlled environment chambers. In the absence of the pollutant, two pollution-resistant clones maintained consistently lower daytime diffusive conductance (LDC) than did a highly susceptible clone or two moderately resistant clones. Differences in LDC among the latter three clones were not significant. At 0.2 microliter per liter SO₂, LDC decreased in the susceptible clone after 8 hours fumigation while the LDC of the other clones was not affected. Fumigation with 0.5 microliter per liter SO₂ decreased LDC of all five clones during the fumigation. Rates of recovery following fumigation varied with the clone, but the LDC of all clones had returned to control values by the beginning of the night following fumigation. Night LDC was higher in the susceptible clone than in the other clones. Fumigation for 16 hours (14 hours day + 2 hours night) with 0.4 microliter per liter SO₂ decreased night LDC by half. Sulfur uptake studies generally confirmed the results of the conductance measurements. The results show that stomatal conductance is important in determining relative susceptibility of the clones to pollution stress.

Resistance to environmental stress may be a result of stress avoidance, stress tolerance, or both (14). Avoidance of air pollution stress might be characterized by maintenance of continuous, low stomatal conductance or rapid stomatal closure during stress. Since stomata regulate water vapor loss and CO₂ uptake, stress-induced alterations in stomatal response may directly influence plant growth and the capacity of plants to respond to additional environmental factors. Between- and within-species variation has been shown in stomatal response to environmental stress. Differences in leaf diffusion resistance response of several *Populus* clones to leaf water potential, light intensity, VPD, and temperature have been reported (17). Two genotypes of cotton (*Gossypium hirsutum*) differed in the response of stomata to water deficits, and the response differences were heritable (21).

Because stomata are the principal portals for entry of air pollutants into plants, considerable interest has been shown in stomatal response to air pollutants. Low stomatal conductance in the presence of phytotoxic pollutants may confer resistance on a plant through avoidance of uptake. Lower conductance in ozone-resistant varieties than in susceptible varieties has been reported for tobacco (23), onion (8), and kidney beans (7). No consistent differences in stomatal conductance were found between resistant and susceptible cultivars of perennial ryegrass (1). The principal reason for differences in SO₂ resistance among several *Cucurbita* cultivars was the relative rate of gas absorption (4).

Karnosky (13) demonstrated wide differences in susceptibility of several *Populus tremuloides* clones to air pollutants and concluded that such differences were under genetic control. He found that five clones (clones 1, 2, 8, 9, 10 in the present study) exposed to 0.5 μl l⁻¹ SO₂ had 34, 5, 6, 4, 3, and 0.5% of leaves injured per plant, respectively. We have conducted experiments with some of the same clones used by Karnosky (13) in an effort to understand the basis of air pollution resistance. The present experiments compared leaf conductance, boundary layer conductance, and sulfur accumulation of five of these clones to determine the contribution of pollution avoidance to pollution resistance. Further studies compared conductance as a function of leaf age to show whether age-dependent differences in pollutant susceptibility within a plant could be due to differences in rates of pollutant uptake.

MATERIALS AND METHODS

Growth of Plants. Stock plants of five *Populus tremuloides* Michx. clones were obtained from the Cary Arboretum, Millbrook, NY. From these, cuttings from stump and root sprouts were rooted under mist and transplanted to a 3:1 sand:loam: Perlite mixture in 12-cm pots. Plants were grown for 10 to 12 weeks in growth chambers under the following environmental conditions: photoperiod 16 h; quantum flux density, measured with a Lambda Quantameter, 350 ± 25 μE m⁻² s⁻¹ PAR at the top of the pots from cool-white fluorescent and incandescent lamps; 25°C day/15°C ± 2°C night temperature; and 70–90% RH. Temperature and RH were measured with a hygrothermograph. Plants were watered to excess once daily with half-strength Hoagland solution and once daily with deionized H₂O. LPI were calculated weekly for each plant (9). Two days before fumigation, plants of each clone were selected for uniformity of size and plastochron index and randomly assigned to three fumigation chambers of the University of Wisconsin Biotron.

Fumigation Chambers. The fumigation chambers were 75 × 75 × 105 cm Plexiglas boxes mounted in slightly larger chambers containing air-mixing equipment and filters. Filtered air flowed in a single pass from a mixing plenum below the floor, through the chamber, and out through the perforated polyvinylchloride pipe 10 cm below the chamber top. The air exchange rate was 6.6 × 10⁻³ m⁻³ s⁻¹. Small fans suspended from the exit pipe maintained air turbulence. The chambers were fitted with glove ports for use during fumigations. SO₂ was introduced into the mixing plenum from tanks of 1,000 or 2,000 μl 1⁻¹ SO₂ in N₂, controlled by a
SO$_2$ EFFECTS ON STOMATAL BEHAVIOR

Environmental conditions in the fumigation chambers were similar to those in the growth chambers. Temperatures were 25 ± 1 °C; RH was maintained at 70 ± 5%. Air temperature was controlled and monitored with a solid state humidity sensor (Thunder Scientific, Albuquerque, NM) and was also monitored for 15 min/h in each chamber with a wide-range Dunmore-type LiCl sensor (Hygrodynamics Hygrometer, American Instrument Co., Silver Spring, MD). Quantum flux densities of 350 ± 25 μE m$^{-2}$ s$^{-1}$ were provided by two 400 w HID lamps (Sylvania Lumalux 2) and five 25 w incandescent bulbs, and were measured before and after each experiment with a Lambda Quantameter. SO$_2$ concentrations in each chamber were measured with Thermo Electron pulsed fluoroscent SO$_2$ analyzers. The SO$_2$ analyzers were calibrated biweekly with a Bendix 888961D calibrator using NBS-traceable standard gas.

Leaf Conductance Measurements. Diffusive conductance of leaves with LPI between 10 and 15 was measured with a Lambda Autoporometer and LI-20S horizontal sensor calibrated according to McCree and Van Bavel (16). The sensor was stored over potassium acetate in the control chamber between measurements to maintain humidity and thermal equilibrium. Measurements taken on abaxial leaf surfaces were converted to conductance, disregarding adaxial conductance which approached zero for all clones.

Adaxial boundary layer conductance was calculated from the rate of water loss from absorbent paper leaf models (11). The models were of green blotting paper with the adaxial surfaces coated with paraffin to eliminate adaxial evaporation and were cut to the size and shape of representative leaves of each clone. The models were glued to Populus tremuloides petioles; the petioles were inserted into a plastic stem at mean canopy height; and the models were wetted with deionized H$_2$O. After temperature equilibration, the rate of weight loss was measured continuously with a Mettler electronic balance installed in the fumigation chamber. Leaf and air temperatures were measured with 0.025 mm Ewanohm-Constantan thermocouples. Boundary layer conductances were calculated using the conversion:

$$g_n = \frac{Q}{C_l - C_a}$$

where Q is the rate of water loss from the model during the linear portion of weight loss versus time curves. Boundary layer conductance was measured ten times on three leaf models of each clone.

Stomatal Conductance of Fumigated and Control Plants. Stomatal conductance was determined every 2 or 3 h on three leaves of two plants of each clone and chamber. Measurements were initiated at 07:00 on the day before fumigation (day 1) and continued until 07:00 the day after fumigation (day 3). The plants were fumigated with 0, 0.2, or 0.5 μL l$^{-1}$ SO$_2$ from 09:00–17:00 on day 2. Day 1 served as a control day and allowed comparison of chamber effects while day 2 allowed comparison of treatment effects. At the beginning and end of each photoperiod, rates of stomatal opening and closure were evaluated from conductance determined at 5-min intervals on different leaves of each clone. During night measurements, a green safelight was used to permit recording of data. The experiment was repeated three times. Data were compared by analysis of variance at each time and by Tukey's Studentized range test (22). Rates of stomatal opening and closing were not statistically analyzed.

Sulfur Uptake. Plants of clones 1, 9 and 10 were fumigated for 8 h with 0, 0.2 or 0.5 μL l$^{-1}$ SO$_2$ with three plants per clone and were treated in a completely randomized design. Growth chamber and fumigation chamber conditions were as given above. Imme-

![Fig. 1. Leaf diffusive conductance versus time for 5 clones of Populus tremuloides L. fumigated with 0 (●), 0.2 (○) or 0.5 (□) μL l$^{-1}$ SO$_2$ on day 2 from 09:00 (1) to 17:00 (†). Dark period is denoted by the bar (—). Each point is the mean of 3 replicate experiments with 3 leaves of each of 2 plants per clone sampled at each time (n = 18). Points marked with * are significantly different from control values at the same time (Tukey's Q, α=0.05). Dotted lines are interpolations from data taken at 5-min intervals at the beginning and end of each photoperiod. (A) Clone 9; (B) clone 1; (C) clone 2; (D) clone 10; (E) clone 8.](image-url)
Table 1. Stomatal and Boundary Layer SO₂ Conductance and SO₂ Uptake Rates of Fumigated Plants

<table>
<thead>
<tr>
<th>Clone</th>
<th>SO₂ Conc.</th>
<th>Stomatal Conductance to SO₂</th>
<th>Boundary Layer Conductance to SO₂</th>
<th>SO₂ Uptake Rate</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>μl l⁻¹</td>
<td>cm s⁻¹</td>
<td>cm s⁻¹</td>
<td>ng cm⁻² s⁻¹</td>
</tr>
<tr>
<td></td>
<td>09:00</td>
<td>12:00</td>
<td>15:00</td>
<td>09:00</td>
</tr>
<tr>
<td>1</td>
<td>0.2</td>
<td>0.682 a,⁎</td>
<td>0.641 a</td>
<td>0.607 ab</td>
</tr>
<tr>
<td>2</td>
<td>0.5</td>
<td>0.704 a, 0.252 c</td>
<td>0.218 cd</td>
<td>0.166 d</td>
</tr>
<tr>
<td>8</td>
<td>0.2</td>
<td>0.458 d, 0.515 b</td>
<td>0.493 b</td>
<td>0.39 a</td>
</tr>
<tr>
<td>9</td>
<td>0.2</td>
<td>0.076 a, 0.704 a</td>
<td>0.636 a</td>
<td>0.48 b</td>
</tr>
<tr>
<td>10</td>
<td>0.5</td>
<td>0.539 abc, 0.487 b</td>
<td>0.263 c</td>
<td>0.292 c</td>
</tr>
</tbody>
</table>

* Values within a column without the same letter are significantly different at α = 0.05 (Tukey’s Q).

RESULTS

Injury Due to SO₂. Fumigation with 0.2 μl l⁻¹ SO₂ caused injury only to plants of clone 1. Up to one-third of the area of older leaves (LPI > 15) was necrotic within 24 h after fumigation was started. Scattered necrotic patches <0.5 cm in diameter appeared on leaves used for conductance measurements (10 ≤ LPI ≤ 15) within 10 h after the start of fumigation. Injury was very extensive on clone 1 plants following fumigation with 0.5 μl l⁻¹ SO₂. All leaves with LPI > 10 showed some injury, and the extent of injury usually increased with LPI. In previous experiments, we observed injury to clone 1 plants after 12 h of fumigation with 0.1 μl l⁻¹ SO₂.

After fumigation with 0.5 μl l⁻¹ SO₂, clone 2 plants had scattered necrotic areas and flecks on older leaves (LPI > 12). Clone 9 plants had scattered small flecks on leaves with LPI > 15. In contrast, clone 8 and 10 plants had no leaf lesions.

Leaf Diffusive Conductance. Diffusive conductances differed among clones and as a result of treatments (Fig. 1, a-e). During the 24 h prior to fumigation, no significant differences in conductance were observed between plants of a clone in different chambers, but differences among clones were significant (α<0.05). During most daylight sampling periods, conductances of plants of clones 9, 1 and 2 did not differ significantly from each other but were significantly greater than those of clones 8 and 10.

Preliminary experiments suggested that leaf conductances during the dark period differed among clones. In the present experiments, leaf conductances of clone 1 plants were greater than those of other clones in the dark. Leaf conductances of all plants declined rapidly after the lights were turned off, and increased gradually throughout the night. The rate of stomatal closure of clone 1 plants was substantially lower than that of the other clones. Stomatal opening in the morning was very rapid in all clones, and little difference could be observed among clones.

Diffusive conductances were calculated for each treatment. Plants were fumigated for 8 h. Data were calculated from H₂O vapor conductance at 09:00, 12:00 and 15:00 h.

<table>
<thead>
<tr>
<th>Clone</th>
<th>Stomatal Conductance to SO₂</th>
<th>Boundary Layer Conductance to SO₂</th>
<th>SO₂ Uptake Rate</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>μl l⁻¹</td>
<td>cm s⁻¹</td>
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<td>12:00</td>
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<td>0.263 c</td>
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* Values within a column without the same letter are significantly different at α = 0.05 (Tukey’s Q).
conductance determinations. The $SO_2$ uptake rate was calculated as

$$Q_{SO_2} = \frac{C_{SO_2}}{g_{a, SO_2}} \cdot \frac{1}{g_{a, SO_2}}$$

The internal $SO_2$ concentration was assumed to be zero.

At 0.2 $\mu$l l$^{-1}$ $SO_2$, uptake rates of $SO_2$ were lowest in the two low conductance clones (8 and 10). The uptake rate of $SO_2$ into clone 1 plants was not reduced at 0.2 $\mu$l l$^{-1}$ since the decline in stomatal conductance was not observed until after the end of the fumigation period (Fig. 1b). At 0.5 $\mu$l l$^{-1}$ $SO_2$, uptake rates into leaves of all clones were high at the start of fumigation (09:00) but rapidly declined to values similar to uptake rates at 0.2 $\mu$l l$^{-1}$ (e.g., clone 2 at 15:00 h).

**Sixteen-Hour Fumigation.** Stomatal conductance of plants of clone 1 was higher in the dark than for the other clones (Fig. 1). Inasmuch as this suggested that dark period uptake of pollutant could be significant, we investigated the effects on clone 1 plants of 8 h (day) and 16 h (14 h day + 2 h night) fumigations with 0.4 $\mu$l l$^{-1}$ $SO_2$. Figure 2 shows that fumigation at 0.4 $\mu$l l$^{-1}$ $SO_2$ for 8 h caused stomatal closure to a degree similar to that shown in Figure 1b at 0.5 $\mu$l l$^{-1}$. Stomatal conductance at night and on the following morning was not significantly altered by this treatment. In contrast, fumigation continued for a longer period caused a highly significant ($a < 0.01$) decrease in leaf conductance throughout the night, and recovery was not complete by the following morning.

**Stomatal Conductance and LPI.** Within a plant of a given clone, sensitivity to $SO_2$ increased with LPI. To determine whether within-plant variation in stomatal conductance could account for these differences, we measured leaf conductance as a function of LPI in unfumigated plants of each clone (Fig. 3). Within-plant variation in susceptibility to $SO_2$ was not due to differences in diffusive conductance. On the basis of leaf conductance, lower leaves (LPI=14) should be injured less than younger leaves (8≤LPI≤14), particularly in clones 1, 2 and 9. This pattern persisted over time of day (Fig. 4), although it was not as pronounced at later times. When plants of clone 1 were fumigated with 0.4 $\mu$l l$^{-1}$ $SO_2$ (Fig. 5), the greatest effect on stomatal conductance was on leaves with LPI between 10 and 17. The response of older leaves was much less pronounced. During fumigation, conductance was highest in the leaves that had just achieved full expansion. These data show that within-plant variations in susceptibility are due largely to differences in pollution tolerance rather than pollution avoidance.

**Sulfur Uptake.** The S content of unfumigated plants of clone 1 was substantially lower than that of clones 9 and 10 (Table II).

![Fig. 2. Leaf diffusive conductance versus time for plants of clone 1 exposed to 0 (O) or 0.4 $\mu$l l$^{-1}$ $SO_2$ for 8 (O) or 16 (C) h from 09:00 (1) to 17:00 (1) or 25:00 h (t). Each point is the mean of determinations of 3 leaves of 4 plants per treatment (n = 12).](image)

![Fig. 3. Leaf diffusive conductance versus LPI for each clone. Data were collected between 12:00 and 14:00 h in the growth chamber. Each point is the mean ± se of measurements of 4 plants of each clone (n = 4). LPI = 0 represents an expanding leaflet 2 cm long.](image)

![Fig. 4. Leaf diffusive conductance versus LPI for clone 1 at 12:00 h, 15:00 h, 18:00 h and 21:00 h. Each point is the mean of measurements on 5 plants on 2 consecutive days (n = 10) and the same plants were used at each time. Measurements were made in the growth chamber.](image)

Plants fumigated with 0.2 or 0.5 $\mu$l l$^{-1}$ $SO_2$ contained more S than unfumigated plants, but the difference was not significant for clone 10 plants at 0.2 $\mu$l l$^{-1}$ $SO_2$. After fumigation with 0.5 $\mu$l l$^{-1}$ $SO_2$, S content of all clones had increased by 0.68 to 0.81 mg S g$^{-1}$ leaf dry weight.

When clone 1 and clone 9 plants were fumigated with 0.1 $\mu$l l$^{-1}$ $SO_2$ for 144 h, S content of both clones increased gradually, with the increase somewhat greater in clone 1 plants (Table III) due to an apparent decline in S content of clone 9 plants.

**DISCUSSION**

Stomata are the principal mediators of gas flux into and out of leaves and the direct action of stress factors and guard cells causes...
feedback effects that reduce stomatal aperture and thus may alleviate the stress (19). Pallardy and Kozlowski (18) showed that stomata of different Populus clones varied in their capacity to respond to VPD and to changes in light intensity. In the present study, differences were shown among aspen clones in rates of stomatal closure when lights were turned off (compare clone 9 in Fig. 1a with clone 1 in Fig. 1b). Differences among clones in stomatal response to SO$_2$ were observed, but above a threshold concentration which varied with clone, pollution stress caused a reduction in stomatal conductance of all clones.

When aspen plants were exposed to SO$_2$, stomatal closure occurred at 0.2 µl/l SO$_2$ (clone 1) or 0.5 µl/l SO$_2$ (all clones). After 8 h exposure to 0.5 µl/l SO$_2$, stomatal conductance of all clones rapidly returned to that of unfumigated plants during the subsequent night period. Return of leaf conductance values in fumigated plants of clone 1 to those of unfumigated plants occurred despite extensive injury to leaves, indicating independent effects of SO$_2$ on guard cells and on mesophyll cells. When clone 1 plants were fumigated for 16 h (Fig. 2), conductance values had not returned to control levels by the next day, suggesting either persistent changes in guard cell metabolism or an interaction between guard cells and subjacent damaged mesophyll cells.

Clonal differences in stomatal conductance below the threshold SO$_2$ concentration for effects on stomata were observed. Lower gas exchange rates were maintained by plants of clones 8 and 10 throughout the day than by those of other clones. Comparing SO$_2$ uptake rates of clones 9 and 10 (Table I), SO$_2$ concentrations would have to be about 20% greater for clone 10 plants to take up the same amount of SO$_2$ as those of clone 9, provided that the concentration remained below the threshold for direct guard cell response.

All five clones responded to 0.5 µl/l SO$_2$ by reducing stomatal conductance to about 0.4-0.6 cm$^2$ s$^{-1}$, and this would cause a greatly reduced SO$_2$ uptake into the leaves. An increase in SO$_2$ concentration to about 2 µl/l would be required to overcome this feedback effect, and such an increase might result in further stomatal closure. Despite this decrease in conductance, injury to clone 1 plants was extensive at 0.5 µl/l SO$_2$. Calculated rates of SO$_2$ uptake during fumigation suggest that injury occurred despite lower uptake of SO$_2$ by leaves of clone 1 plants than by those of clones 9 or 10 (Table I). However, uptake during the first 3 h of fumigation may have been higher in clone 1 plants at 0.5 µl/l SO$_2$ than in the other clones, depending on the rate or guard cell response to SO$_2$. We have not yet measured rates of stomatal response during the initial period of exposure.

During a long-term, continuous fumigation (Table III), S uptake appeared to be higher in clone 1 than in clone 9. Since daytime conductances in both clones were similar in other experiments (Fig. 1), the higher uptake in clone 1 plants may be due to the higher night conductances in this clone (Fig. 1). If 0.1 µl/l SO$_2$ was below the threshold for further night stomatal closure such as in Figure 2. However, most of the differences can be attributed to the apparent decline in S content of clone 9.

In Levitt’s (14) terminology, clones 8 and 10 appear to avoid stress, while differences in stress resistance among clones 1, 2 and 9 are due to differences in stress tolerance. Although clone 1 plants reduced pollutant uptake by stomatal closure at 0.5 µl/l SO$_2$, uptake rate of SO$_2$ into the leaf was still sufficient to cause extensive injury. The remaining clones also reduced pollutant uptake, but SO$_2$ uptake rates were sufficiently low that extensive

Table II. Sulfur Content and Net Sulfur Uptake of Leaves of Three Aspen Clones Exposed to SO$_2$ for 8 Hours

<table>
<thead>
<tr>
<th>SO$_2$ concn. µl l$^{-1}$</th>
<th>Clone 1</th>
<th>Clone 9</th>
<th>Clone 10</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.2 net</td>
<td>0.31</td>
<td>0.32</td>
<td>0.24</td>
</tr>
<tr>
<td>0.5 net</td>
<td>0.78</td>
<td>0.81</td>
<td>0.68</td>
</tr>
</tbody>
</table>

* Difference between treatment and control means.

b Difference significant at $\alpha = 0.05$ (Tukey’s Q).

$^a$ Not significant.

Table III. Sulfur Content and Net Sulfur Uptake of Leaves of Two Aspen Clones Exposed to 0 or 0.1 µl/l SO$_2$ for 144 h

<table>
<thead>
<tr>
<th>Day</th>
<th>Control Treatment</th>
<th>Fumigation Treatment</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Gross</td>
<td>Gross</td>
</tr>
<tr>
<td></td>
<td>Clone 1</td>
<td>Clone 9</td>
</tr>
<tr>
<td>1</td>
<td>2.34 ± 0.15</td>
<td>4.03 ± 0.15</td>
</tr>
<tr>
<td>2</td>
<td>1.89 ± 0.19</td>
<td>4.18 ± 0.15</td>
</tr>
<tr>
<td>3</td>
<td>1.92 ± 0.12</td>
<td>4.13 ± 0.20</td>
</tr>
<tr>
<td>4</td>
<td>1.96 ± 0.12</td>
<td>3.79 ± 0.19</td>
</tr>
<tr>
<td>5</td>
<td>1.88 ± 0.14</td>
<td>3.75 ± 0.20</td>
</tr>
<tr>
<td>6</td>
<td>1.86 ± 0.17</td>
<td>3.85 ± 0.22</td>
</tr>
</tbody>
</table>

* Not significant.

b Difference between control and treatment means significant at $\alpha = 0.05$.

c Difference between control and treatment means significant at $\alpha = 0.01$. 

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injury to mesophyll cells did not occur.

These data suggest that stress avoidance may involve two types of responses at the stomatal level: passive avoidance, the maintenance of low gas exchange capacity under favorable as well as unfavorable conditions; and active avoidance, the capacity to respond to environmental stress by reducing gas exchange during stress periods. Active avoidance may be a metabolically active process or a manifestation of injury to guard cells.

Within a plant, SO₂ injury was usually directly proportional to leaf age, as has been observed in some other studies (6). These age-dependent differences could not be explained on the basis of differences in leaf conductance. This agrees with the findings of Bressan et al. (4) that within-plant variations in pollutant susceptibility are not due to differences in uptake rates.

SO₂ either induced stomatal closure or elicited no stomatal response in our experiments. In contrast, several investigators reported that SO₂ increased leaf conductance or transpiration (2, 15). Others observed stomatal closure during fumigation with SO₂ (20). Black and Black (3) reported that stomatal opening in Vicia faba leaves was associated with destruction of epidermal cells adjacent to the stomata. They suggested that guard cells may be protected from SO₂ uptake by the cuticles of these cells. Differences in stomatal response of various species could be explained on the basis of differences in the relative SO₂ susceptibility or uptake rates of guard cells and adjacent epidermal cells. Stomatal closure may be observed in species with higher uptake rates into guard cells while stomatal opening may occur in species with more resistant guard cells. Differences in environmental conditions and SO₂ dosages may also be important.

LITERATURE CITED