The Influence of Exposure Temperature and Relative Humidity on the Response of Pinto Bean Foliage to Sulfur Dioxide

D. L. Rist and D. D. Davis

Former graduate student and associate professor, respectively, Department of Plant Pathology and Center for Air Environment Studies, The Pennsylvania State University, University Park, PA 16802. Current address of senior author: Department of Plant Pathology, Cornell University, Ithaca, NY 14853.

Contribution 1007 of the Department of Plant Pathology and 476-77 of the Center for Air Environment Studies. Journal Series Paper 5408 of the Pennsylvania Agricultural Experiment Station. Supported by Environmental Protection Agency Grant T900537.

Space was provided by the School of Forest Resources, The Pennsylvania State University.

Accepted for publication 10 August 1978.

ABSTRACT

RIST, D. L., and D. D. DAVIS. 1979. The influence of exposure temperature and relative humidity on the response of pinto bean foliage to sulfur dioxide. Phytopathology 69: 231-235.

When 20-day-old pinto bean plants (*Phaseolus vulgaris* 'Pinto 111') were exposed to 0.9 ppm sulfur dioxide (SO_2) the amount of trifoliolate leaf injury induced by SO_2 generally was greater at 32 C than at either 13 or 21 C, and greater at 80% relative humidity (RH) than at 40 and 60% RH. However, injury was less following exposures at 32 C for 1 hr and 21 C for 1 and 2 hr than that caused by equivalent exposures at 13 C. Stomatal conductance increased significantly with increased temperature and RH. Stomatal conductance of trifoliolate leaves from plants exposed to SO_2 was less than that of exposed control plants. The foliar content of SO_2, evaluated after exposures at 21 and 32 C, generally was greater at the higher temperatures.

The rate at which plant foliage absorbs sulfur dioxide (SO_2) is an important factor in determining the amount of foliar injury resulting from this phytotoxicant. Factors which influence stomatal behavior, and thereby affect the rate of pollutant uptake, accordingly influence the phytotoxicity of SO_2 (22). In general, stomatal aperture has been found to be directly related to RH (15,18) and temperature (25,33). However, the extent of this relationship is dependent on other factors such as light and plant species (6).

There are few published accounts evaluating the impact of varying atmospheric temperature and moisture regimes on plant sensitivity to SO_2. Swain (26) and Wells (32) both concluded that plants were more tolerant to SO_2 at exposure temperatures of 5 C or less than at higher temperatures. Swain (26) further added that varying the temperature above 5 C did not significantly influence plant sensitivity to SO_2. Setterstrom and Zimmerman (22) also reported that no significant difference in injury of buckwheat plants occurred following individual exposures to SO_2 at 18 and 40 C. Field exposure of conifers to SO_2 in late November resulted in less injury than did similar fumigations 1 mo earlier (9).

O'Gara (16) concluded that plants generally were three times more tolerant to SO_2 at 30% RH than at 100% RH. Variations between 50 and 75% RH did not affect the sensitivity of wheat, oats, barley, or rye to SO_2 (22); likewise, SO_2 injury to alfalfa was not significantly influenced by varying RH from 40 to 70% (28). Katz (9) reported slight injury to conifers from field exposures to SO_2 at 60% RH, and no symptoms from exposures at 45% RH.

Bonte and Louguet (2) found that greater foliar injury occurred on Pelargonium exposed to SO_2 in moist air than in dry air. Schramel (21) reported that stomatal resistance and SO_2 uptake of *P. vulgaris* 'Tenderlong OK' was related to soil moisture content, but he did not detect a direct influence of SO_2 on diffusive resistance of the stomata. Markowski et al (14) found that *P. vulgaris* 'Tenderlong OK' foliage exposed to SO_2 under optimum soil conditions had 200% the sulfur content of unexposed control plants.

The primary objective of this study was to evaluate critically the influence of ambient temperature on macroscopic symptoms, stomatal conductance, and sulfur content as a measure of uptake of SO_2 by pinto bean foliage. A second objective was to evaluate critically the influence of atmospheric moisture on macroscopic symptoms and stomatal conductance.

MATERIALS AND METHODS

Cultural conditions.—Pinto bean seeds were germinated in trays of vermiculite in controlled environment chambers maintained at 23 C and 75% RH. Two days following cotyledon emergence, seedlings of uniform development were transplanted, two per 950-ml plastic pot containing a mixture of peat:perlite:soil (1:1:1, v/v) which was amended with 113 g super phosphate, 113 g limestone, 43 g dolomitic limestone, and 14 g potassium nitrate per 35 liters. The transplanted seedlings subsequently were grown for 13 days in controlled environment chambers at the above conditions, with a 12-hr photoperiod of 25 klux beginning at 0600 hours.

Effect of sulfur dioxide and temperature on macroscopic symptom expression, stomatal conductance, and sulfur content.—Sets of 40 20-day-old plants were exposed to 0.9 ± 0.1 ppm SO_2 at 13, 21, or 32 ± 1C at 75 ± 2% RH within a modified controlled environment chamber. Subsets of 10 plants were selected randomly from the 40 and exposed for either 1, 2, 3, or 4 consecutive hr, beginning at 1000 hours, at each temperature. Ten unexposed control plants were included in each experiment and were kept under similar environmental conditions. This SO_2 concentration corresponded to 2,502, 2,395, or 2,292 $\mu g/m^3$ at each temperature, respectively. The conductometric SO_2 monitor used in these experiments was calibrated periodically with permeation tubes (17). Following exposure to SO_2, the plants were placed on a greenhouse bench. Four days later, the percentage of injured tissue was estimated visually on a 0-100% scale in increments of 10; in addition values of 1, 5, 95, and 99 were included at the extremes. Symptoms were evaluated on each unifoliolate and the first two trifoliolate leaves. This experiment was replicated three times at each of the three temperatures.

An electrical diffusion porometer (29) was used in a second set of experiments to determine the stomatal conductance, as well as the leaf temperature, of bean leaves exposed to SO_2. Following exposure, plants were returned to growth chambers at 23 C and 75% RH. The stomatal conductance rate was measured on the abaxial surface of the terminal leaflet of the first trifoliolate leaf of

00031-949X/79/000039$03.00/0

each plant. Conductance rates were measured prior to SO_2 exposure at 0800, 0900, and 0950 hours; at 30-min intervals during exposure from 1000 to 1400 hours; following exposure at 1700 and 2000 hours; and similarly on sets of 10 nonexposed control plants subjected to the same temperature and humidity regimes. Because the growth chamber lights were turned off automatically at 1800 hours, the measurements at 2000 hours were taken in the dark. These experiments were replicated two times.

In a third set of experiments, the sulfur (S) content of foliar tissue of exposed and unexposed control plants was determined. Exposures similar to those described above were conducted at either 21 or 32 C with RH maintained at 75%. Immediately following exposure for either 1, 2, 3, or 4 consecutive hr, sets of 10 plants were removed from the exposure chamber and the unifoliolate and first two trifoliolate leaves were harvested. The two unifoliolate leaves from each plant were combined, as were the first two trifoliolate leaves. Harvested leaves were allowed to wilt to insure stomatal closure. The leaves then were rinsed in a tepid solution of Ivory Snow detergent and distilled water for 15 sec, and again in pure distilled water for 5 sec. Leaves were dried for 38 hr at 80 C. The dried material was ground and analyzed for total S content on a dry weight basis with a calibrated Leco Sulfur Analyzer (8) and iodometric titration (3). This experiment was replicated three times at both temperatures.

Effect of sulfur dioxide and atmospheric moisture on macroscopic symptom expression and stomatal conductance.—The impact of varying atmospheric moisture on the response of pinto bean plants to SO_2 was determined in a fourth set of experiments as in the preceding section, except that the temperature within the exposure chamber was held constant at 21 C while the RH was maintained at 40, 60, or 80%. After exposure, the plants were returned to growth chambers set as described previously. Symptoms were rated 4 days later.

The influence of atmospheric moisture on the stomatal conductance rate of pinto beans was determined as described previously for the temperature studies. Experiments were conducted at 21 C with humidity regimes of 60 and 80% RH.

Because the data were not distributed normally, the statistical significance ($P = 0.05$) of differences between treatments in the first and fourth experiments was determined with the nonparametric Mann-Whitney test (7). Data in the remaining three experiments were analyzed by analysis of variance with Waller and Duncan's modified (Bayesian) least significant difference test (31) ($P = 0.05$).

RESULTS

Symptoms.—Two types of foliar symptoms were observed on bean plants following exposure to SO_2. The most common symptom type on both unifoliolate and trifoliolate leaves was the typical acute injury pattern: light tan, interveinal and/or marginal necrosis. The second type, observed only on the trifoliolate leaves, was a white or reddish-brown stipple on the adaxial leaf surface similar to that induced by ozone. However, the latter type of injury was observed only occasionally.

Effect of sulfur dioxide and temperature on macroscopic symptom expression.—Generally, pinto bean plant foliage was most tolerant to SO_2 when exposed at 13 or 21 C, and most sensitive when exposed at 32 C (Fig. 1). The unifoliolate leaves were much less sensitive to SO_2 at this plant age than were the trifoliolate leaves. The only significant injury on the unifoliolate leaves occurred following 4 hr of exposure to SO_2 at 32 C. Trifoliolate leaves also were much more responsive to changes in exposure temperature. A 1-hr exposure at 21 or 32 C did not result in trifoliolate leaf injury, whereas a 1-hr exposure at 13 C resulted in a median trifoliolate leaf injury of 5%. After 2 hr of exposure at 13 C, the trifoliolate leaves exhibited significantly greater injury than those exposed for 2 hr at 21 C. However, after 3 and 4 hr of exposure there was no significant difference in injury between plants exposed to SO_2 at 13 and 21 C. Exposures at 32 C resulted in greater trifoliolate injury after 2, 3, and 4 hr of exposure as compared to trifoliolate leaves exposed at 13 or 21 C. These results were consistent in all three replications.

Effect of sulfur dioxide and temperature on stomatal conductance.—Prior to exposure, the stomatal conductance measured at 0800, 0900, and 0950 hours was not statistically different among plants in the growth chamber. The stomatal conductance of control plants and plants exposed to SO_2 increased approximately tenfold when moved from the growth chamber at 23 C into the exposure chamber at 32 C. The stomatal conductance of all plants exposed to SO_2 eventually decreased in comparison to unexposed control plants at the same temperature (Fig. 2). The significant decrease in conductance of exposed versus control plants was first detected after 3 hr (at 1300 hours) of exposure at 32 C, whereas it was detected after 1 hr (at 1100 hours) of exposure at 21 C. Three hours after exposure (at 1700 hours) the stomatal conductance was equal for control plants from both experiments conducted at 21 and 32 C. Plants exposed to SO_2 at 21 C showed a significant decrease in conductance at this time. Plants exposed to SO_2 at 32 C had significantly lower conductances than plants of all other treatments at this time.

Effect of sulfur dioxide and temperature on sulfur content of leaves.—The S content of unexposed unifoliolate leaf tissue was about 0.30% on a dry weight leaf tissue basis, and was significantly greater than the normal S content of about 0.24% of the trifoliolate leaf tissue. The S content of trifoliolate leaves equalled or exceeded that of the unifoliolate leaves after 2 hr or more of exposure to SO_2 at either 21 or 32 C.

The S content of both unifoliolate and trifoliolate leaves following exposure to SO_2 at 32 C generally was greater than the S content of leaves exposed at 21 C (Fig. 3). The S content of unifoliolate leaves was significantly greater following 3 and 4 hr of exposure at 32 C than after 3 and 4 hr at 21 C (Fig. 3). However, there was significantly less S in these leaves after 4 hr of exposure at 32 C than after 3 hr of exposure at 32 C. The S content of trifoliolate leaves exposed to SO_2 at 32 C was significantly greater than that of trifoliolate following 2, 3, and 4 hr of exposure at 21 C.

Effect of sulfur dioxide and atmospheric moisture on macroscopic symptom expression and stomatal conductance.—Trifoliolate leaf injury was significantly greater after 2, 3, and 4 hr

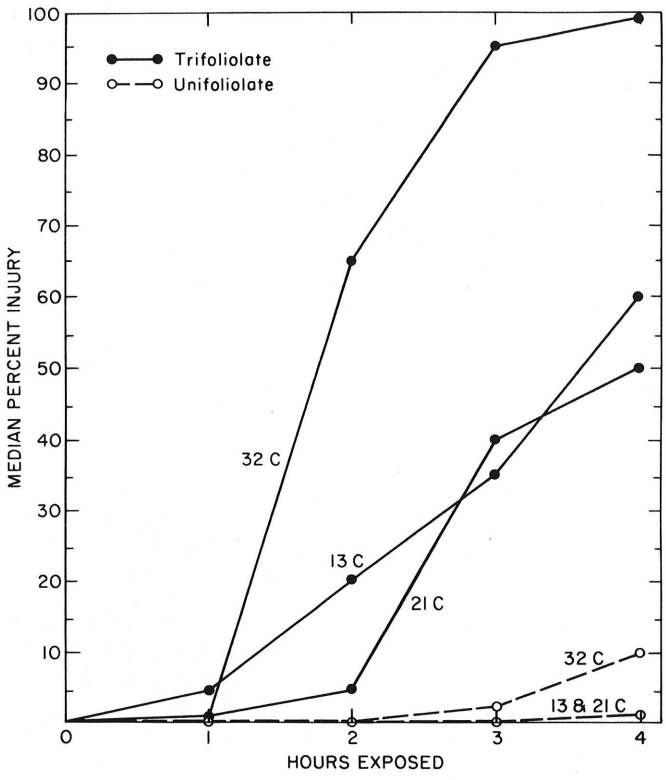

Fig. 1. Median percent injury of trifoliolate and unifoliolate leaves of pinto bean plants exposed to 0.9 ppm sulfur dioxide (SO_2) for either 0, 1, 2, 3, or 4 hr at three temperatures.

of exposure at 80% RH than at either of the lower humidities (Fig. 4). Very little foliar injury was induced at 40 or 60% RH. Plants placed in the exposure chamber at 80% RH, with or without SO_2, showed an increase in conductance whereas those at 60% RH revealed significant decreases in conductance (Fig. 5). A significant decrease in conductance in response to SO_2 was first detected after 2.5 hr of exposure (1230 hours) at 80% RH, and after 4 hr of exposure (1400 hours) at 60% RH. At 1700 hours the conductance of plants exposed to SO_2 at 80% RH was less than that of all other plants.

DISCUSSION

The bifacial, interveinal, and marginal necrosis observed on pinto bean leaves in these experiments were typical acute symptoms of SO_2 injury to broadleaved plants (1). In contrast to previous reports (5,22,26,32), the results of this study illustrate that critically controlled exposure temperatures between 13 and 32 C dramatically influenced the sensitivity of pinto beans to SO_2 (Fig. 1). The generally greater sensitivity of the foliage at 32 C vs. 21 and 13 C may be explained at least partially by increased pollutant uptake at the higher temperature.

The significant increase in injury after 1 hr of exposure at 13 C compared to an equivalent dose at either 21 or 32 C, and after 2 hr at 13 vs. 21 C, was not expected. Thomas and associates (27,28) have reported that SO_3 is the form of S most toxic to plants and the subsequent oxidation of $SO_3^=$ to $SO_4^=$ reduces this toxicity by approximately 30-fold. Further evaluation of the influence of temperature on the oxidation rate of $SO_3^=$ to $SO_4^=$ within bean leaf tissue, coupled with the fact that temperature influenced the SO_2 absorption rate (Fig. 3), may help explain these temperature-mediated differences in sensitivity.

Our observations that stomatal conductance increases with increasing temperature (Fig. 2) is consistent with previous reports (15,25,33). Once the stomatal aperture is at a maximum, changes in the conductance readings are entirely related to vapor pressure deficit (VPD). The greater VPD at 32 C vs. 21 C may account for the large increase in conductance at the higher temperature (Fig. 2). Because the conductance of SO_2 would not be influenced by the VPD, the absorption of SO_2 will not necessarily be proportional to the observed increases in stomatal conductance of water vapor.

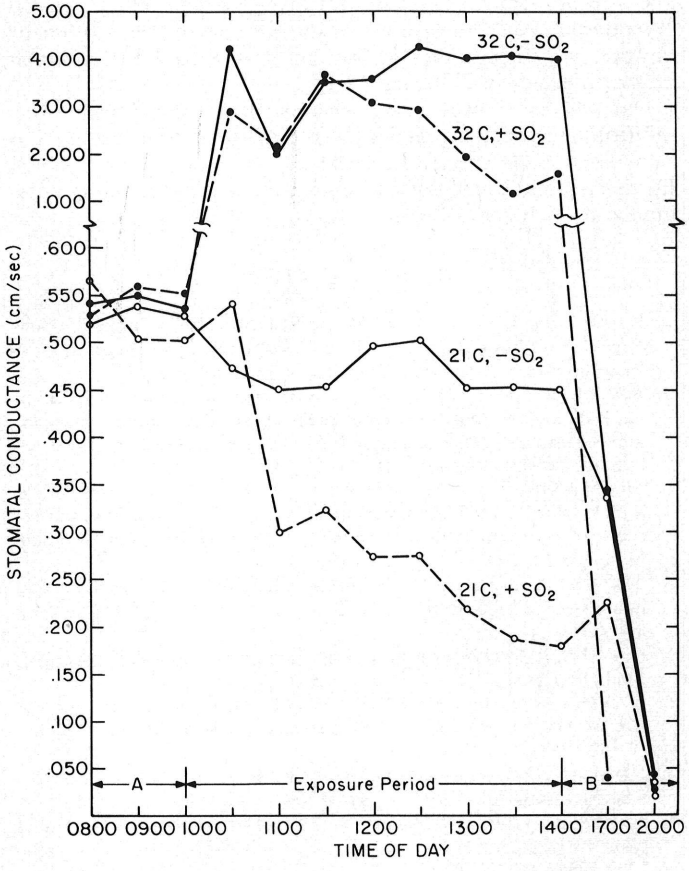

Fig. 2.-(A, B). Stomatal conductance of the apical leaflet of the first trifoliolate leaf of pinto bean plants under various conditions. **A)** Pre-exposure conductance, at 23 C, 75% RH, and light intensity of 25 klux. Exposure period: conductance at 75% RH, light intensity of 25 klux, and temperature as designated. Dashed lines represent the conductance of leaves exposed to 0.9 ppm SO_2. Solid lines represent the conductance of unexposed controls. **B)** Postexposure conductance at 23 C, 75% RH. Lights off at 1800 hours.

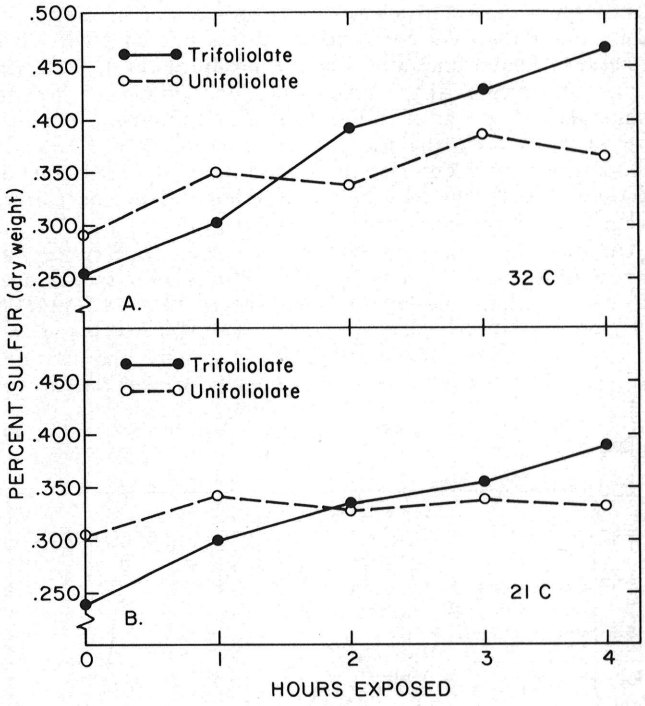

Fig. 3-(A, B). Percent sulfur (dry weight) in trifoliolate or unifoliolate leaves of pinto bean plants following 0, 1, 2, 3, or 4 hr of exposure to 0.9 ppm SO_2 at **A)** 32 C or **B)** 21 C.

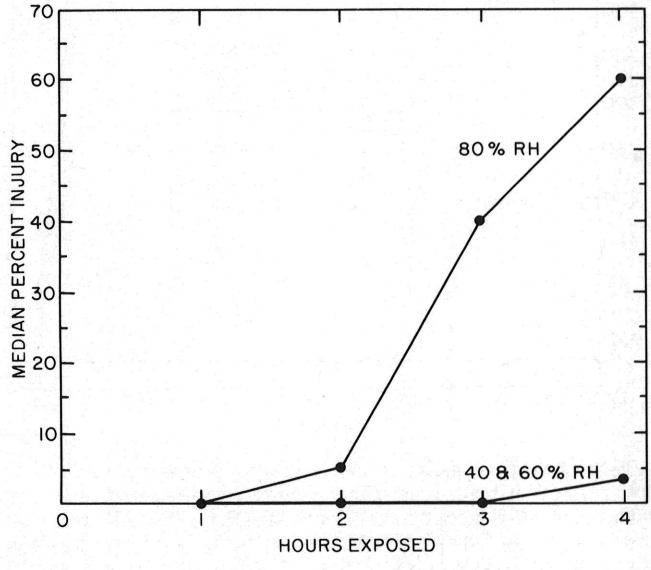

Fig. 4. Median percent injury of trifoliolate leaves of pinto bean plants exposed to 0.9 ppm SO_2 for either 0, 1, 2, 3, or 4 hr at three levels of relative humidity.

The decrease in conductance of plants exposed to SO_2 at both 21 and 32 C probably was due to stomatal closure (Fig. 2). This observation was in contrast to reports of SO_2-stimulated stomatal opening in corn and broad bean (10–12,30), but was in agreement with the results of Sij and Swanson (23) who worked with pinto bean. Sulfur dioxide was reported to increase stomatal aperture of broad bean leaves at RH above 40%, but decreased the opening at RH below 40% (13). Sulfite inhibition of photosynthetic enzymes and resultant internal CO_2 increases (15,34) may have been related to the stomatal closure. Further evaluation of the interactive influence of temperature and SO_2 on internal CO_2 concentrations may clarify such findings.

The stomatal conductance of plants exposed to SO_2 remained lower than their respective control plants 3 hr after removal from the exposure chamber (Fig. 2). At this time, the conductance of the most severely injured plants, ie, those exposed at 32 C, was significantly lower than the conductance of less injured plants. The decrease in conductance after 1 hr of exposure at 21 C (Fig. 2) was not accompanied by appreciable visible injury on similarly treated plants until after 3 hr of exposure (Fig. 1). Conversely, the high level of injury occurring after 2 hr of exposure at 32 C was not accompanied by a decrease in conductance until after 3 hr of exposure (Fig. 1). This indicates that SO_2-induced stomatal closure was not entirely coincident with visible injury.

Variations in sorption of SO_2 and the subsequent S concentrations in foliage have been attributed to differences in species, age, SO_2 concentration, and environmental factors (19,20,24). Paul (19) has shown that the S content of bean leaves (*P. vulgaris* 'Sensation') increased steadily when exposed to SO_2 at various concentrations for up to 72 hr. This increase was directly proportional to the concentration of SO_2. Markowski et al (14) also reported that the sulfur content of *P. vulgaris* 'Tenderlong OK' was greater following exposure to 0.5 ppm SO_2 than at 0.3 ppm for 14 days. We evaluated SO_2 absorption (as measured by increased S concentrations of surface-cleaned leaf tissue) over much shorter exposure periods, but found a similar incrase in total S of both unifoliolate and trifoliolate leaves (Fig. 3).

The increase in S content of trifoliolate leaves was equivalent at both 21 and 32 C after 1 hr of exposure (Fig. 3). This suggests that the increase in stomatal conductance at 32 C is mainly related to the increase in the VPD at the higher temperature and not to a significant increase in stomatal aperture. The increase in sensitivity to SO_2 at 32 C vs. 21 C is therefore more likely caused by the delay in stomatal closure (Fig. 2). The faster rate of SO_2 uptake by the trifoliolate compared to the unifoliolate leaves is similar to that reported by Paul (19), and may explain the greater sensitivity of the former (Fig. 1). Differences in tissue age may be related to this difference in SO_2 uptake (4).

Our findings generally agree with reports that indicate SO_2 injury is directly related to the amount of atmospheric moisture (2,16,22,26). Our results support the concept that humidity influences the rate of gaseous exchange of pinto bean leaves. When plants were moved from the growth chamber at 75% RH into the exposure chamber at 60% RH there was significant decrease in stomatal conductance. Conversely, plants placed in the exposure chamber at 80% RH showed a significant increase in conductance (Fig. 5). Injury was directly related to conductance rates. As with temperature, changes in humidity influence the VPD, and are therefore involved in the variations in conductance described above.

Schramel (21) reported that SO_2 visibly increased stomatal aperture but had no effect on diffusive resistance of *P. vulgaris* 'Tenderlong OK.' He gave no reason for this apparent anomaly; however, the use of a pressure porometer may have influenced his ability to detect such changes.

Our results showed that, when stringent control of other influential factors was practiced, variations in temperature and RH significantly influenced the sensitivity of pinto beans to SO_2. Further studies are needed to determine if these results are not limited to such controlled conditions.

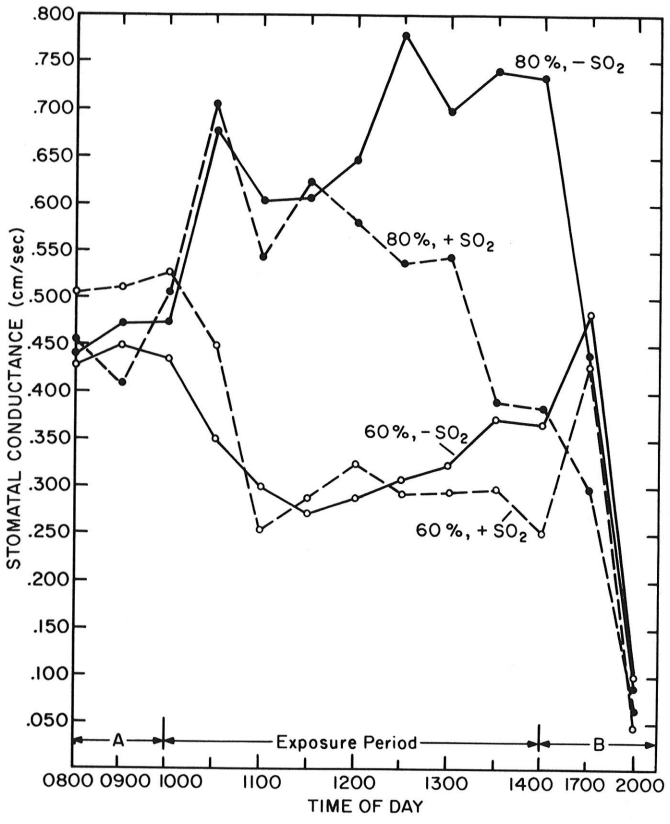

Fig. 5-(A, B). Stomatal conductance of the apical leaflet of the first trifoliolate leaf of pinto bean plants exposed to various environmental conditions. **A)** Pre-exposure conductance at 23 C, 75% RH, and light intensity of 25 klux. Exposure period: conductance at 21 C, light intensity of 25 klux, and RH as designated. Dashed lines represent the conductance of leaves exposed to 0.9 ppm SO_2. Solid lines represent the conductance of leaves from unexposed controls. **B)** Postexposure conductance, at 23 C and 75% RH. Lights off at 1800 hours.

LITERATURE CITED

1. BARRETT, R. W., AND H. M. BENEDICT. 1970. Sulfur dioxide. Pages C1-C17 *in* Recognition of Air Pollution Injury to Vegetation: A Pictorial Atlas. Air Pollut. Control Assoc., Pittsburgh, PA.
2. BONTE, J., and P. LOUGUET. 1975. Interrelations entre la pollution par le dioxyde de soufre et le mouvement des stomates chez le Pelargonium × hortorum: effets de l'humidité relative et de la teneur en gaz carbonique de l'air. Physiol. Vég. 13:527-537.
3. BREMANIS, E., J. R. DEERING, C. F. MEADE, and D. A. KEYWORTH. 1967. Elimination of nitrogen and chloride interferences in the iodometric determination of sulfur as sulfur dioxide. Materials Res. Standards 7:549-560.
4. CRACKER, L. E., and J. S. STARBUCK. 1973. Leaf age and air pollutant susceptibility: Uptake of ozone and sulfur dioxide. Environ. Res. 6:91-94.
5. DAINES, R. H. 1968. Sulfur dioxide and plant response. J. Occupat. Med. 10:516-524.
6. DAVIES, W. J., and T. T. KOZLOWSKI. 1973. Stomatal responses of five woody angiosperms to light intensity and humidity. Can. J. Bot. 52:1525-1534.
7. HOLLANDER, M., and D. A. WOLFE. 1973. Nonparametric Statistical Methods. John Wiley & Sons, New York. 503 p.
8. JONES, J. B., and ISAAC, R. A. 1972. Determination of sulfur in plant tissues using a Leco sulfur analyzer. J. Agric. Food Chem. 20: 1292-1294.
9. KATZ, M. 1939. Fumigation experiments on conifers in their natural habitat. Pages 218-243 *in* Effect of Sulfur Dioxide on Vegetation, Nat. Res. Council Bull. 815. 447 p.
10. MAJERNIK, O., and T. A. MANSFIELD. 1970. Direct effect of SO_2 pollution on the degree of opening of stomata. Nature 227:337-378.
11. MAJERNIK, O., and T. A. MANSFIELD. 1971. Effects of SO_2 pollution on stomatal movements in Vicia faba. Phytopathol. Z. 71:123-128.
12. MAJERNIK, O., and T. A. MANSFIELD. 1972. Stomatal response to

raised atmospheric CO_2 concentrations during exposure of plants to SO_2 pollution. Environ. Pollut. 3:1-7.
13. MANSFIELD, T. A., and O. MAJERNIK. 1970. Can stomata play a part in protecting plants against air pollution? Environ. Pollut. 1: 149-154.
14. MARKOWSKI, A., S. GRZESIAK, and M. SCHRAMEL. 1975. Susceptibility of six species of cultivated plants to sulphur dioxide under optimum soil moisture and drought conditions. Bull. Polish Acad. Sci. 22:889-898.
15. MEIDNER, H., and T. A. MANSFIELD. 1968. Physiology of Stomata. McGraw-Hill, New York. 179 p.
16. O'GARA, P. J. 1917. American Smelting and Refining Company's tests with sulfur and sulfuric acid on soil. Mining Sci. Press 114:840-843.
17. O'KEEFE, A. E., and G. C. ORTMAN. 1966. Primary standards for trace gas analysis. Anal. Chem. 38:760.
18. OTTO, H. W., and R. H. DAINES. 1969. Plant injury by air pollutants: Influence of humidity on stomatal aperture and plant response to ozone. Science 163:1209-1210.
19. PAUL, R. 1976. Aspects quantitatifs de l'absorption foliare du SO_2 par Phaseolus vulgaris L. Proc. 4th Int. Colloq. on Control of Plant Nutrit. 1:73-82.
20. ROBERTS, B. 1974. Foliar sorption of atmospheric sulfur dioxide by woody plants. Environ. Pollut. 7:133-140.
21. SCHRAMEL, M. 1975. Influence of sulphur dioxide on stomatal apertures and diffusive resistance of leaves in various species of cultivated plants under optimum soil moisture and drought conditions. Bull. Polish Acad. Sci. 23:57-63.
22. SETTERSTROM, I. C., and D. W. ZIMMERMAN. 1939. Factors influencing susceptibility of plants to sulfur dioxide injury. Contrib. Boyce Thompson Inst. 10:155-181.
23. SIJ, J. M., and C. A. SWANSON. 1974. Short-term kinetic studies on the inhibition of photosynthesis by sulfur dioxide. J. Environ. Qual. 3:103-107.
24. SPEDDING, D. J. 1966. Uptake of sulfur dioxide by barley leaves at low concentrations. Nature 224:1229-1230.
25. STAFELT, M. G. 1962. The effect of temperature on stomatal opening. Physiol. Plant. 15:772-779.
26. SWAIN, R. E. 1923. Atmospheric pollution by industrial wastes. Indust. Eng. Chem. 15:296-301.
27. THOMAS, M. D., R. H. HENDRICKS, T. R. COLLIER, and G. R. HILL. 1943. The utilization of sulphate and sulfur dioxide for the sulfur nutrition of alfalfa. Plant Physiol. 18:345-371.
28. THOMAS, M. D., and G. R. HILL. 1935. Absorption of sulphur dioxide by alfalfa and its relation to leaf injury. Plant Physiol. 10:291-307.
29. TURNER, N. C., F. C. PEDERSEN, and W. H. WRIGHT. 1969. An aspirated diffusion porometer for field use. Conn. Agric. Exp. Stn. Spec. Bull. Soils XXIX/100. 13 p.
30. UNSWORTH, M. H., P. V. BISCOE, and H. P. PINCKEY. 1972. Stomatal response to SO_2. Nature 239:458-459.
31. WALLER, R. A., and D. B. DUNCAN. 1969. A Bayes rule for the symmetric multiple comparison problem. J. Am. Stat. Assoc. 64:1484-1503.
32. WELLS, A. E. 1917. Results of recent investigations of the smelter smoke problem. Indust. Eng. Chem. 9:640-646.
33. WILSON, C. C. 1948. The effect of some environmental factors on the movements of guard cells. Plant Physiol. 23:5-37.
34. ZEIGLER, I. 1972. The effect of SO_3 on the activity of ribulose-1,5-diphosphate carboxylase in isolated chloroplasts. Planta 103:155-163.