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Inheritance of Resistance to Sulfur Dioxide in Cucumber¹

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Abstract. Crosses and subsequent segregation between inbred lines of 'National Pickling cucumber (*Cucumis sativus* L.) resistant to acute exposure to sulfur dioxide, and the sensitive 'Chipper' cucumber indicated that resistance was dominant and may be controlled by a single gene.

Sulfur dioxide is a constituent of the atmosphere usually occurring naturally at less than 2 $\mu\text{l liter}^{-1}$ (16), is closely related to bound sulfite, a normal intermediate in the sulfur assimilation pathway of plants (21, 20) and can serve as a sulfur source for sulfur-starved plants (9). Sulfur dioxide becomes harmful at unusually high concentrations, such as may rise from the combustion of coal. Chronic exposure to moderately elevated levels of SO_2 inhibits plant growth and is subtly injurious (10). An acute exposure (usually more than 0.5 $\mu\text{l liter}^{-1}$ for up to 24 hr) produces interveinal necroses and water-logged lesions (14, 1).

Heritable differences in resistance to injury from either chronic (3) or acute (18, 13, 12, 17, 15) exposure to SO_2 occur within plant species, so the possibility of breeding plants for resistance to SO_2 exists. Resistance of onions to ozone was found to be determined by a dominant gene. Resistance of *Phaseolus vulgaris* to ozone was recessive (4), and attributed to

fewer stomata on leaves of resistant plants (5).

In a study of differences in resistance among the Cucurbitaceae we found that inbred 'National Pickling' (NP) cucumber was more resistant to acute exposure to SO_2 than an inbred line derived from 'Chipper' (CH) (6, 7). The dose response curve of NP to SO_2 was markedly sigmoidal, so that, at a certain level of exposure to SO_2 (3.3 $\mu\text{l liter}^{-1}$ for 16 hr), more than 5 times as much leaf area of CH sustained injury on the average than did NP. However, there was progressively less difference in the responses of NP and CH at higher SO_2 exposures. This observation gave us reason to expect that a rather distinct classification of phenotype for individual plants seemed possible if exposure conditions were selected to produce the maximum difference in response. The objective of this study was to determine the inheritance of SO_2 resistance using a cross between the resistant NP and the susceptible CH.

NP was developed at Michigan State University and inbred breeder's seed was used. CH, also known as SC 25, was developed at Clemson University. Seed was produced at Michigan State University from breeders' stock seed by repeated selfing. Seed used for experiments had been selfed at least through 5 generations.

Groups of 6 plants of NP and CH were cross-pollinated in the greenhouse by standard methods (19) and the F_1 , F_2 and

backcrosses to both parents were produced.

SO_2 reaction test. For testing of each population, plants were grown as described earlier (22) in 350 cc plastic pots containing a mixture of 1 soil:1 peat:1 turface, (v/v/v). After emergence, the plants were thinned to 1 per pot, and were watered twice a day with half-strength Hoagland's nutrient solution. The plants were grown in a Conviron Model E15 growth chamber programmed to produce 30°C with 50% relative humidity and 9mW cm^{-2} at the temperature peak of the light period of 15.5 hr; and 15°C with 95% relative humidity at the bottom of the temperature trough of the dark period. Seeds of the parents and various crosses were planted each day, so that the fumigations, which were performed daily on plants 5-6 weeks old, all could be done on plants of about the same age.

A group of 4 or fewer plants of each parent or cross was fumigated in a single chamber each day. When available, a control group of CH plants of the same age was fumigated under identical conditions in an adjacent chamber. Fumigations were performed as previously described (6) for 20 hr with the air entering the chamber containing SO_2 at 3 $\mu\text{l liter}^{-1}$. After fumigation, the pots were placed in pans containing water and allowed to stand for 24 hr at 21°C in a laboratory illuminated by Cool White fluorescent lamps. The percentage of leaf area showing necrosis was determined visually as described previously (6).

The SO_2 sensitive CH plants developed necroses on an average of 33% of their leaf area, and NP plants developed necroses on an average of 5.7% of their leaf area, in good agreement with our earlier observations (6). However, variation in the response of individual plants of CH resulted in overlapping response ranges of CH and NP. (Table 1). Since each plant resulting from a cross had to be judged either resistant or sensitive to SO_2 , the point of minimum overlap in the distributions of the response was chosen as the resistance criterion. Plants which sustained necroses on less than 20% of their leaf area were defined as resistant, and plants which sustained necroses on

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Table 1. Distributions of injury level among NP and CH plants exposed to SO₂ in air at 3 μl l⁻¹ for 20 hours.

Pedigree	Generation	Total	Distribution of plants						R (0-20% necrosis)	S (21+ necrosis)	Expected ratio ^a R:S
			Leaf necrosis								
			0-10%	11-20%	21-30%	31-40%	41-50%	50+			
NP	P ₁	20	17	3				20	0	1:0	
CH	P ₂	16	1	2	4	3	3	3	13	0:1	
NP × CH	F ₁	19	16	2	1			18	1	1:0	
CH × NP	F ₁	4	4					4	0	1:0	
F ₁ × NP	BC ₁	24	12	9	1	2		21	3	1:0	
F ₁ × CH	BC ₂	24	7	6	2	4	2	13	11	1:1	
	F ₂	16	11	3	1		1	14	2	3:1	

^aAssuming a single dominant gene for resistance.

20% or more of their leaf area were defined as sensitive.

Based on this criterion, the SO₂ resistance of NP was dominant in the F₁ crosses, regardless whether NP was the pollen or seed parent (Table 1). Susceptible plants segregated in the backcross of CH and in F₂ populations (Table 1). The observed frequencies of occurrence of sensitive plants in these populations were close to those expected if the sensitivity of CH was determined by a single recessive gene.

All breeding lines in the cucumber breeding program at Michigan State University are sensitive to SO₂, while the rather old cultivar, NP, is resistant (Table 2). Presumably, somewhere in the course of selection of superior horticultural traits, an indirect selection for sensitivity to SO₂ occurred. Because SO₂ resistance is dominant and apparently monogenic, the transfer of SO₂ resistance from NP to other genetic backgrounds should be achievable with relative ease.

The relative resistances of 4 cucurbit cultivars, including NP and CH, to SO₂ were shown in our earlier study to be due to differences in rates of absorption of SO₂ (6). NP absorbs SO₂ more slowly than does CH when exposed to the same concentration. The same pattern of relative resistances was evident (although the magnitude of the difference between NP and CH was less) in a second test of SO₂ resistance: emission of ethane in response to exposure of leaf discs to bisulfite solutions (7). Since bisulfite in solution ap-

pears to enter the discs through the cut edges rather than through the stomates, the manifestation of the resistance differences in leaf discs floated on bisulfite solutions indicates that the resistance differences are not attributable to stomatal differences. Another barrier, one which would affect uptake of both SO₂ and bisulfite, e.g. the plasma membrane, is presumed to be responsible for the resistance difference. This interpretation is supported by the finding that the relative resistances of the 4 cucurbit cultivars to several stresses likely to affect membrane properties (chilling, heating, alcohols, mechanical injury, desiccation) were the same as for exposure to SO₂ or bisulfite (8).

It is not surprising that genetic analysis of SO₂ resistance or resistance to other toxic gases are not performed routinely. The techniques for selection and classification of phenotypes are complex and require considerable instrumentation. It was critical to compare plants of the same age because of changes in leaf sensitivity with age and to give the plants a precise exposure to SO₂ because of the narrow exposure range over which the difference in response of NP and CH is maximal. The further constraint of being able to fumigate no more than 8 plants per day with the equipment available to us necessitated daily plantings. Several months were required to accumulate sufficient data for genetic analysis.

A more rapid method of phenotypic classification, suitable for simultaneous characterization of large numbers of plants, is needed to facilitate breeding for genetically determined resistance to SO₂ into crop species. Elsewhere, we have described such an assay: the emission of ethane from leaf discs exposed to bisulfite (7). This test may expedite the SO₂ selection procedure and permit screening of large populations used in breeding programs.

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Table 2. Sensitivities of various cucumber lines and hybrids to sulfur dioxide. Plants were fumigated with an influx concentration of 3.5 μl l⁻¹ SO₂ for 16 hr.

Genotype	No. plants	Mean necrosis (%)
CH	12	36
MSU 581	8	41
GY 14	12	40
MSU 183G	8	39
GY 14 × MSU 581	12	37
GY 14 × CH	12	45
MSU 183G × NP	8	31
NP	4	6