Ozone and Sulfur Dioxide Effects on Reproduction and Host-Parasite Relationships of Selected Plant-Parasitic Nematodes

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ABSTRACT

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The effects of air pollution on the reproduction of five species of plant-parasitic nematodes with different feeding habits and host effects were studied by exposing soybean or begonia hosts to ozone (O_3) and sulfur dioxide (SO_2), singly or in combination, and to charcoal filtered (control) air. Exposure of infected soybean plants to O_3 and an O_3-SO_2 mixture inhibited reproduction and development of *Heterodera glycines* and *Paratrichodorus (Nanidorus) minor*, but the increase of *Belonolaimus longicaudatus* usually was unaffected. Exposure of soybean host plants to SO_2 enhanced the reproduction of *Pratylenchus penetrans* compared with that in plants exposed to the charcoal filtered air control or to O_3. Foliar injury of begonia by O_3 or an O_3-SO_2 mixture inhibited the increase of *Aphelenchoides fragariae*. The suppresive effects of *A. fragariae* were greater in leaves pre-exposed to O_3 or an O_3-SO_2 mixture before rather than after leaves were inoculated with nematodes. The growth of nematode infested soybean plants and leaves of begonia was inhibited by O_3 and the O_3-SO_2 mixture compared with that of similar control plants grown in the presence of nematodes and charcoal filtered air. Nodulation of soybean plants inoculated with *B. longicaudatus* and *P. minor* was suppressed by O_3 and the O_3-SO_2 mixture. The inhibition of nodulation of soybean by *H. glycines* was extensive; the pollutants had no further detectable effect.

Additional key words: Glycine max, Rhizobium japonicum, Begonia sp., air pollutants.

The effects of air pollutants on host-parasite interactions involving nematodes has not been studied extensively. Populations of saprophagous and predaceous nematodes were greater in areas of forests severely damaged by SO_2 and alkaline particulate material than in those that were slightly damaged (2).

Other soil organisms also are affected by air pollutants (7). Ozone inhibited nodulation by *Rhizobium japonicum* Kirch. on roots of *Glycine max* (L.) Merr. (18,24) and *Phaseolus vulgaris* L. (13). Ozone increased the abundance of *Fusarium* sp. associated with roots of *P. vulgaris* (13), but did not increase *Fusarium oxysporum* Schlecht. on roots of *Brassica oleracea* L. (11). Industrial effluents, presumably composed of SO_2 and particulates, have been implicated in the abnormal development of mycorrhizae in forest species damaged by these pollutants (21).

The present study was initiated to determine: whether exposure of soybean to O_3 and SO_2, singly and in combination, would influence reproduction of root-parasitic nematodes with different feeding habits; whether exposure of begonia leaves to these pollutants would affect a foliar nematode; and whether growth and nodulation of soybean parasitized by selected nematode species would be

altered by the pollutants. The effects of O_3 and SO_2, singly or in combination, on the growth of soybean in the absence of nematodes is the subject of another paper (D. E. Weber et al, unpublished).

MATERIALS AND METHODS

Soybeans. *Plant culture.* Seven-day-old seedlings of soybean (*Glycine max* [L.] Merr. 'Dare') were grown from seed in sand. Seedlings were transplanted one to a plastic pot filled with white sand containing 100 mg of commercial *Rhizobium japonicum* inoculum. Pots, 13 cm in diameter, were used in experiments that lasted 48 days. Pots 20 cm in diameter were used in experiments that lasted 67 or 79 days. An additional 100 mg of *Rhizobium* inoculum was added per pot during transplanting. Sifted 500-μm (35-mesh) sand was used in tests with *Heterodera glycines* Ichinohe; 246-μm (65-mesh) sand was used in all other studies. Plants were grown in a greenhouse at 24 ± 6 C and received approximately 100 ml of half-strength Hoagland's nutrient solution minus nitrogen twice each week. Plants were grown in a minimum of 10-hr photoperiods. Flowering was inhibited by interrupting the night period with 3 hr of illumination from eight 150-W incandescent lamps.

Nematode culture and inoculations. The following nematode species were studied on soybean: a sedentary semiendoparasite, *Heterodera glycines* Ichinohe (race 1); two migratory ectoparasites, *Belonolaimus longicaudatus* Rau, and *Paratrichodorus (Nanidorus) minor* (Colbran, Seddiqi) Loof (=*Trichodorus christiei* Allen); and a migratory endoparasite, *Pratylenchus penetrans* (Cobb) Filip. and Schuum.-Stekh.

Inoculum of *H. glycines* was maintained on Lee soybean. Cysts were removed from roots by a high-pressure spray of water and collected on a 250-μm (60-mesh) screen. Eggs were obtained by crushing cysts in a Ten Broeck homogenizer. Roots of test plants were inoculated with 9,000 eggs per plant in investigations that involved nematode reproduction.

Belonolaimus longicaudatus was cultured on Lee soybean or strawberry (*Fragaria virginiana* Duch. 'Earlibelle'). *P. minor* was obtained from Lee soybean or corn (*Zea mays* L. 'Pioneer 3369A'). Nematodes were extracted by decanting and sieving of infested soil. Roots were inoculated with approximately 400 *B. longicaudatus* and 100 *P. minor* per plant in studies involving both single and mixed populations of these species.

Inoculum of *P. penetrans* was extracted from Lee soybean roots by the Seinhorst mist technique (20). Roots of test plants were inoculated with 1,900 nematodes per plant.

All soybean seedlings were inoculated separately with each species at 15 days from seeding. Calibrated suspensions of each nematode species was poured into indentations in the sand that exposed soybean roots. The roots were covered with additional sand.

Air pollutant treatments. Soybean plants were exposed to the pollutants or charcoal-filtered air in 12.5-m^3 exposure chambers (8) adapted for greenhouse use. Exposures were made at two periods relative to the time of inoculation. Four initial pollutant exposures were made within a 1-wk period prior to nematode inoculations. Seedlings were exposed to approximately 490 μg O_3/m^3 (25 pphm) and 655 μg SO_2/m^3 (25 pphm), singly or in combination, and to charcoal-filtered air for four daily 4-hr periods. Seedlings then were inoculated with nematodes. Subsequent exposures were made in 4-hr periods on 3 alternate days per week until experiments were terminated. Plants remained in chambers under continuous circulation of charcoal-filtered air between exposure periods. Ozone concentrations were monitored by Mast O_3 analyzers which were calibrated to 1% buffered KI. Sulfur dioxide was measured with a Davis SO_2 analyzer. Since SO_2 interferes with the measurement of O_3, a chromium trioxide scrubber (19) was used to remove SO_2 from the O_3 sample probe of the chamber that received mixtures of O_3 and SO_2.

Experimental design. Soybean plants were grouped into units of three to five plants per nematode-pollutant combination. Units were completely randomized within chambers. Except for the single test with *P. penetrans*, all experiments were repeated at least once. Similar procedures were used except that egg inoculum density of *H. glycines* was increased to 16,500 per plant in the second trial. Because the results of given trials of experiments were similar, data from only one group of studies are presented.

Evaluation procedures. The influences of the pollutants on soybean plants and population densities of nematodes were evaluated by an analysis of variance. Fresh weights of shoots and roots of soybean were measured following harvests at 36, 48, 67, 79, or 89 days after nematode inoculations. Nodules on roots were counted.

Penetration of soybean roots by *H. glycines* was determined 8 days after inoculation. Roots of plants were removed from pots and stained with acid-fuschin lactophenol. After clearing in lactophenol, the number of larvae in the roots were counted. Other experiments involving *H. glycines* were terminated 36 and 67 days after inoculation. Cysts were washed from roots by high-pressure spray, collected on a 250-μm (60-mesh) screen, and the numbers of cysts per plant were determined. The numbers of males in 100-g subsamples of sand were counted (4).

Experiments with *B. longicaudatus* and *P. minor* were terminated 48 and 79 days after inoculation. Numbers of nematodes per pot were determined from 100-g subsamples of sand by sugar flotation-sieving (4) and the numbers of nematodes per gram fresh weight of root were calculated.

Reproduction of *P. penetrans* was evaluated 89 days after inoculation. Nematodes were collected by placing infected soybean roots in Seinhorst mistifiers (20) for 16 days. Population densities per plant and nematodes per gram fresh weight of roots were calculated. The numbers of nematodes in soil were determined by sugar flotation-sieving (4).

Begonia. *Plant culture.* Rooted cuttings of *Begonia* sp. 'Schwabenland Red' were transplanted into 20-cm-diameter plastic pots containing a peat-perlite (1:1, v/v) mix. Plants were grown in a greenhouse at 25 ± 5 C and received weekly applications of Peters' 20-20-20 (1.9 g/L) nutrient solution.

Foliar inoculations. Seven weeks after the begonia cuttings were transplanted, four leaves per plant were each inoculated with 150 *Aphelenchoides fragariae* (Ritzema-Bos) Christie extracted from alfalfa "callus" cultures. Nematodes were applied in 0.4-ml water suspensions to 2.5 × 3.0-cm strips of cheesecloth which had been placed on the lower epidermis of the leaves. Polyethylene film was attached to the inoculated area by paper clips. Plants were covered with moist cheesecloth and plastic bags to maintain a humid atmosphere, then were placed in an unlighted room for 45 hr. Covers were removed, and when the leaves were dry the plants were randomized on a greenhouse bench.

Air pollutant treatments. Begonia plants were exposed to 490 μg O_3/m^3 and 655 μg SO_2/m^3, singly or in combination, and to filtered air as described for one 4-hr exposure period. Plants were arranged in two groups of three plants for each pollutant; exposures were made 3 days before leaves were inoculated with nematodes or 3 days after inoculation. Plants previously exposed to the pollutants and those scheduled for exposure were placed in the chamber receiving charcoal-filtered air.

Evaluation procedures. Thirty days after the inoculation of begonia leaves with *A. fragariae*, fresh weight of inoculated leaves were obtained, and the type and amount of injury were rated (Table 5). At this time, nematodes were extracted from the leaves in Seinhorst mistifiers (20) over a 12-day period. Nematodes were counted from diluted samples and the total number per leaf was determined.

RESULTS

Soybeans. *Pollutant effects on foliage, growth, and nodulation.* Ozone and the O_3-SO_2 mixture inhibited the growth of soybean both in the presence and absence of nematodes (Tables 1–4). These pollutants also caused chlorosis and necrosis of leaves and an increase in the abscission of trifoliate leaves. Sulfur dioxide inhibited the growth of soybean inoculated with *P. penetrans* (Table 4), but did not injure soybean foliage.

The effects of pollutant-nematode combinations on nodulation varied. Because of the severe inhibition of nodulation of soybean by *H. glycines*, the number of nodules from roots parasitized by this nematode did not differ among the pollutant treatments (Table 1). In contrast, nodulation in plants parasitized by *B. longicaudatus*

and *P. minor* was inhibited by exposure of soybean to O_3 and the O_3-SO_2 mixture, as compared to the control and SO_2-treated plants (Tables 2 and 3).

Pollutant effects on nematodes. Penetration of roots by *H. glycines* at 8 days after inoculation was not affected by the pollutants. Fewer cysts were recovered from soybean exposed to O_3 and the O_3-SO_2 mixture than from the controls or plants exposed to SO_2, but this difference was significant only 67 days after inoculation (Table 1). The suppressive effect on cyst development amounted to an inhibition of 73–77% as compared to the control. The total number of cysts per plant increased over the 36- to 67-day period, but a smaller increase was observed when plants were exposed to O_3 and the O_3-SO_2 mixture. Fewer males developed on soybean exposed to O_3 and the O_3-SO_2 mixture within 67 days after inoculation.

The reproduction of *P. minor* was suppressed by exposure of plants to O_3 or the O_3-SO_2 mixture. This inhibition occurred at 48 and 79 days in experiments involving *P. minor* combined with *B. longicaudatus* (Table 2), and at 48 days in experiments involving single populations of *P. minor* (Table 3). The numbers of *B. longicaudatus*, singly (Table 3) or conbined with *P. minor* (Table 2) were not affected by the pollutants at 48 days. However, at 79 days, the reproduction of *B. longicaudatus* was inhibited when plants were treated with the O_3-SO_2 mixture (Table 2).

The relation between root weights and the number of nematodes was expressed in the number of nematodes per gram fresh weight of roots. On this basis, numbers of *B. longicaudatus* per unit of roots of plants exposed to O_3 or the O_3-SO_2 mixture were greater than on those associated wth SO_2 or the control. In contrast, the numbers of *P. minor* per gram of root on plants exposed to O_3 or the O_3-SO_2 mixture were less than those associated with nonfumigated controls (Tables 2 and 3).

Reproduction of *P. penetrans* was enhanced on plants exposed to SO_2, whereas O_3 had no significant influence (Table 4). The O_3-SO_2 mixture also appeared to enhance *P. penetrans*, but densities were not significantly different from the control.

Begonia. *Host symptomatology.* Ozone alone and in mixture with SO_2 caused several distinct types of leaf injury on begonia: an interveinal bronze coloration, tissue necrosis, dark-brown stippling, and tan spotting. Injury, in percent per leaf, ranged from 38 to 77% (Table 5). Leaves of nonfumigated control plants were not injured.

TABLE 1. The influence of air pollutant SO_2 and O_3 on the growth of soybean and development of *Heterodera glycines*[a]

Treatments[b]	Days after inoculation	Plant fresh weight (g)		Nodules per plant (no.)		Total cysts[d]	Cysts (No. per gram root fr. wt.)	Total males[d]
		With nemas	Without nemas[c]	With nemas	Without nemas[c]			
Control	36	9.4	12.4	4	49	486	108	2,656
	67	24.0	48.6	9	108	1,955	164	
SO_2	36	9.1	11.0	4	46	444	107	2,239
	67	28.4	41.8	17	88	1,738	172	
O_3	36	5.3*[e]	6.4*	3	23*	382	218	356*
	67	4.1*	14.4*	1	45*	525*	353*	
SO_2 + O_3	36	5.8*	5.6*	3	19*	396	182	555*
	67	6.6*	11.2*	9	46*	451*	256	
LSD (P = 0.05)	36	1.9	2.0	NS	14	NS	NS	836
	67	15.5	9.7	NS	12	623	176	

[a]Values are means from five plants.
[b]Concentrations of pollutants were: SO_2 (655 $\mu g/m^3$), O_3 (490 $\mu g/m^3$), and a mixture of 655 μg SO_2/m^3 + 490 μg O_3/m^3.
[c]The effects of the pollutants on soybean plants in the absence of nematodes have been characterized (D. E. Weber, unpublished).
[d]Values calculated from two samples per plant.
[e]Asterisk (*) indicates that values are significantly different (P = 0.05) from the nonpollutant-treated control.

TABLE 2. The influence of SO_2 and O_3 on the growth of soybean and contaminant development of *Belonolaimus longicaudatus* and *Paratrichodorus (Nanidorus) minor*[a]

Treatments	Days after inoculation	Plant fresh weight (g)		Number of nodules per plant		Nematodes per plant (in 1,000's)		Nematodes per gram root fresh weight	
		With nemas	Without nemas[b]	With nemas	Without nemas[b]	*B. longicaudatus*	*P. (N.) minor*	*B. longicaudatus*	*P. (N.) minor*
Control	48	25.6	23.5	53	72	2.8	19.7	383	2,530
	79	74.2	77.7	68	82	14.0	25.5	465	856
SO_2	48	24.4	20.7	42	59	2.4	16.2	303	2,040
	79	83.5	70.7	63	97	11.0	23.6	317	619
O_3	48	8.5*[c]	8.0*	39	32*	2.8	3.6*	826	998*
	79	30.4*	28.7*	46*	44*	11.3	7.1*	917*	556
SO_2 + O_3	48	8.8*	8.6*	35*	27*	2.1	1.8*	1,011	734*
	79	27.8*	20.2*	42*	41*	9.2*	4.0*	864*	363*
LSD (P = 0.05)	48	4.1	5.3	15	22	NS	9.0	NS	1,034
	79	14.7	13.4	14	20	4.7	8.3	285	307

[a]Values are means calculated from data for three plants at 48 days after inoculation and from five plants at 79 days after inoculation.
[b]The effects of the pollutants on soybean in the absence of nematodes have been characterized (D. E. Weber, unpublished).
[c]Asterisk (*) indicates values that are significantly different (P = 0.05) from the nonpollutant-treated control.

Symptoms occurred within 22 hr after a single 4-hr exposure. The predominant symptom for both O_3 or the O_3-SO_2 mixture was a bronze coloration on the upper epidermis of begonia leaves. Necrosis frequently was bifacial.

Pollutant effects on Aphelenchoides fragariae. The damaging effects of air pollutants on begonia foliage inhibited the reproduction of *A. fragariae* (Table 5). This suppression was greater when plants were exposed to the pollutants before inoculation. Injury of inoculated leaves on plants exposed to O_3 and the O_3-SO_2 mixture before inoculation amounted to 77 and 68%, respectively, of the leaf surface at 3 days after exposure. The injury was associated with a suppression in nematode reproduction of 79% for plants exposed to O_3 and 69% for those exposed to the O_3-SO_2 mixture. By contrast, injury of inoculated leaves of plants treated with these pollutants after inoculation ranged from 58% for those exposed to O_3 to 38% for those exposed to the O_3-SO_2 mixture. The injury was associated with a 24 and 38% suppression in the reproduction of nematodes, respectively.

TABLE 3. The influence of SO_2 and O_3 on soybean and development of single populations of *Belonolaimus longicaudatus* and *Paratrichodorus (Nanidorus) minor* at 48 days after inoculation[a]

Treatments	Plant fresh weight (g)	Nodules per plant	Nematodes per plant	Nematodes per gram root fresh weight
B. longicaudatus				
Control	27.2	178	760	61
SO_2	19.3*[b]	179	646	70
O_3	15.9*	58*	603	90
$SO_2 + O_3$	10.8*	58*	815	176*
LSD ($P = 0.05$)	3.5	36	NS	53
P. (N.) minor				
Control	19.3	234	332	41
SO_2	18.6	185*	110*	13*
O_3	12.3*	65*	102*	15*
$SO_2 + O_3$	9.3*	84*	80*	16*
LSD ($P = 0.05$)	2.7	39	162	24

[a]Values are means calculated from data for five plants.
[b]Asterisk (*) indicates that values are significantly different ($P = 0.05$) from the respective nonpollutant-treated controls.

DISCUSSION

These studies demonstrated that plant-parasitic nematodes of various feeding habits respond differently to plant stresses induced by O_3 and SO_2.

In experiments involving *H. glycines*, O_3 and the O_3-SO_2 mixture may have altered the amount and quality of nutrients in syncytia which surround the head region of this sedentary endoparasite. Since *H. glycines* is dependent on nutrients from syncytia, changes in nutrition may have caused the adverse affect on nematode reproduction and development. Furthermore, suppression of the development of males by exposure of plants to O_3 and the O_3-SO_2 mixture probably inhibited fertilization and the development of subsequent nematode generations.

The penetration of soybean roots by larvae of *H. glycines* was not affected by exposure of plants to the pollutants. However, when the numbers of nematodes and the size of roots were considered, the numbers of larvae and cysts per gram of root were increased by exposures of soybean to O_3 and the O_3-SO_2 mixture. A similar increase in nematodes per gram of root also was observed in studies involving *B. longicaudatus*. This relationship can be misleading,

TABLE 4. The effects of SO_2 and O_3 on population development of *Pratylenchus penetrans*[a]

Treatments	Plant fresh weight (g)	Nematodes per plant (in 1,000's)	Nematodes per gram root fresh wt.
Control	126	49.2	886
SO_2	100*[b]	207.6*	5,351*
O_3	84*	33.7	841
$SO_2 + O_3$	47*	64.9	3,172
LSD ($P = 0.05$)	20	84.2	2,421

[a]Values are means calculated from data for five soybean plants.
[b]Asterisk (*) indicates that values are significantly different from the nonpollutant-treated control.

TABLE 5. The effects of the damage of foliage caused by O_3 and SO_2, singly and in combination, on reproduction of *Aphelenchoides fragariae* in leaves of begonia[a]

Treatments[b]	Leaf injury caused by pollutants[c] (%)	Leaf injury and growth influenced by pollutants and nematodes[d]				Reproduction of nematodes[e]	
		Type of Injury[f]	Percent[g]	Injury index[h]	Leaf fresh wt. (g)	Nematodes per leaf (in 1,000's)	Nematodes/g leaf fresh wt. (in 1,000's)
Before inoculation:							
Control	0	1.1	48	53	3.6	43.7	13.2
SO_2	0	1.3	50	70	3.3	39.0	12.5
O_3	77	2.4	86	208	1.9	9.0	5.2
$SO_2 + O_3$	68	2.6	75	196	1.8	13.4	9.0
After inoculation:							
Control	0	1.2	48	59	3.7	45.1	13.5
SO_2	0	1.2	58	67	3.3	43.3	14.4
O_3	58	1.7	72	123	3.3	34.5	10.4
$SO_2 + O_3$	38	1.8	61	115	3.5	27.9	8.8
SE[i]	4	0.2	6	15	0.3	5.2	1.8

[a]Values are expressed as means of 12 inoculated leaves from three plants with four inoculated leaves per plant. Leaves were inoculated with 150 nematodes per leaf.
[b]By utilizing two groups of plants, one group was exposed to the pollutants and nonpolluted air of the control 3 days before inoculation. Another group was treated similarly at 3 days after inoculation.
[c]Injury in percent per leaf was estimated on a scale of 0–100% at 3 days after exposure to pollutants.
[d]Leaf injury and fresh weight were measured at 30 days after inoculation.
[e]Nematodes were extracted from leaves at 30 days after inoculation.
[f]The type of injury was based on a scale of 1–3, where: 1 = reddish-brown tissues, 2 = reddish-brown and necrotic tissues, and 3 = necrotic tissues.
[g]The amount of injury per leaf was estimated on a scale of 0-100%.
[h]The injury index was calculated by multiplying percent injury by the type of injury value.
[i]The standard error (SE) reflects deviations from the means of treatments within both groups of plants.

since it probably was caused by a dilution effect as the amount of root tissues increased in the absence of O_3.

The effects of the stresses of pollution on the host-parasite association of the two migratory-ectoparasitic nematodes, *P. minor* and *B. longicaudatus*, were different, but each species responded similarly in studies involving combined or single populations. The inhibition of *P. minor* by O_3 and the O_3-SO_2 mixture may have resulted from the presence of fewer root tips in the smaller root systems of plants exposed to these pollutants. Since apical areas of roots are more suitable feeding sites for this nematode than other regions of the root (9), a small number of root tips could limit nematode feeding and reproduction. In contrast, *B. longicaudatus* is less specific in regard to feeding sites (22). As a result, the inhibitory effects of the pollutants on the growth of roots did not limit the size of nematode populations.

The enhancement of populations of the migratory-endoparasitic nematode, *P. penetrans*, by SO_2 was similar to that reported for other stresses. For example, the reproduction of *P. penetrans* was stimulated on plants infected with *Verticillium* sp. (15) and *Fusarium* sp. (6).

The inhibitory effects of air pollutants on nematode reproduction apparently were related to foliar injury and the retardant effects of the pollutants on nodulation and plant growth. Ozone is extremely reactive and does not pass through mixtures of sand, peat, and gravel; hence, it is doubtful that this pollutant would directly affect biological activities in soil (3). A direct effect of SO_2 is more likely. Sulfur dioxide is absorbed by soil (1), but this gas reacts with soil water to form hydrogen ions and ions composed of sulfur. These products may influence nematodes and other organisms associated with soil.

The availability and quality of organic and inorganic substances are important factors in the increase of nematode populations (16). If these substances are altered or if nematodes cannot continue to feed within the host, populations are suppressed. Damage of soybean foliage probably modified metabolites translocated to plant roots and associated with the rhizosphere (23). Although evidence is not extensive, O_3 has been implicated in the modification of root metabolites. Kochhar (11) found that O_3 treatment of *Festuca arundinacea* Schreb. resulted in the production of exudates that inhibited growth and nodulation of *Trifolium repens* L. In other studies (14, 23), the concentration of carbohydrates and potassium was lower in roots of plants exposed to O_3 than in those of nonfumigated controls. These metabolic changes could depress the growth and development of plant-parasitic nematodes. Oteifa (17) demonstrated that a deficiency of potassium in the host delayed the initiation of egg production by *Meloidogyne incognita*.

In leaves of begonia, the reproduction of *A. fragariae* was inversely related to the amount of injury to foliage caused by O_3 and the O_3-SO_2 mixture. This relationship probably was due to the destruction of sites for nematode feeding and penetration. Phenolic substances associated with the browning of tissues may have inhibited the penetration of leaves of begonia by *A. fragariae*. These substances have been implicated as probable causes of O_3-induced discoloration of plant foliage (10). They could be a major cause of inhibited reproduction of *A. fragariae*, since brown tissues were evident after the exposure of inoculated leaves to O_3 and the O_3-SO_2 mixture. *A. fragariae* may have contributed further to the inhibition process by influencing the chemical reactions associated with the browning of tissues (5). This response could account for injury of inoculated leaves of plants exposed to SO_2 and the control during the period after exposures were initiated.

Experiments described herein demonstrate different effects of air pollutants on plant-parasitic nematodes as modified by exposure of plant foliage to pollutants. Although foliage injury undoubtedly is related to inhibition of nematode reproduction, the detailed physiological mechanism of the interactions as described remain to be characterized.

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