Response of Tomatoes to Ozone, Sulfur Dioxide, and Infection by *Pratylenchus penetrans*

B. B. Shew, R. A. Reinert, and K. R. Barker

Graduate assistant; plant pathologist, Agricultural Research Service, U.S. Department of Agriculture; and plant pathologist, respectively, Department of Plant Pathology, North Carolina State University, Raleigh 27650.

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ABSTRACT

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Tomato plants (*Lycopersicon esculentum* 'Walter') were inoculated with initial population densities of *Pratylenchus penetrans* ranging 0–4,000 nematodes per pot and were repeatedly exposed for 3 hr to ozone (O_3) doses ranging 0.0–0.4 μl O_3/ L of air (1 μl O_3/ L of air = 1,960 μg O_3/ m^3 of air). In other experiments, tomato plants, uninoculated or inoculated with *P. penetrans,* were exposed (4 hr per exposure) 15 times to 0.2 μl O_3/ L of air, or 0.2 μl SO_2/ L (1 μl SO_2/ L of air = 2,620 μg SO_2/ m^3 of air), or both, or were exposed (3 hr per exposure) to 0.2 μl O_3/ L of air or 0.8 μl SO_2/ L of air, or both. Exposures to charcoal-filtered air served as controls. Decreases in dry weights of plant parts excised from tomato plants exposed to 0.2 μl O_3 per liter of air added to the decrease in dry weight caused by exposure to sulfur dioxide (SO_2) at 0.2 μl/ L of air adequately predicted the decrease in dry weight of tomato plants caused by exposure to 0.2 μl O_3 + 0.2 μl SO_2 per liter of air. When 0.2 μl O_3 and 0.8 μl SO_2 per liter of air were present in mixture, they acted antagonistically and caused less change in leaf and shoot dry weight than could be predicted by the main effects of O_3 or SO_2. The presence of *P. penetrans* attacking the roots enhanced the negative effects of O_3 + SO_2 on leaf growth (dry weight), but suppressed the inhibitory effects of O_3 + SO_2 on axillary shoot dry weight. Treatments containing 0.8 μl SO_2 per liter of air reduced tomato fruit weight, but the amount of reduction was antagonized by the presence of O_3.

Additional key words: air pollutants, pollutant mixtures.

The responses of many cultivated plants to important air pollutants such as ozone (O_3) (9) and sulfur dioxide (SO_2) (13) have been documented and recognition of the resultant yield losses has led to the establishment of air quality standards. Unfortunately, agronomic and horticultural crop species are likely to be grown in environments that simultaneously contain more than one air pollutant. Also, other abiotic and biotic stresses may further reduce the growth and yield of the pollutant-exposed plant. If pollutant× pollutant or pollutant×environment (including pollutant×plant pathogen) interactions occur, air quality standards for single pollutants may not be relevant to the plant-production environment.

Tomato (*Lycopersicon esculentum* Mill.) is sensitive to O_3 (19). Although visible injury of tomato by SO_2 alone occurs only at relatively high concentrations of the pollutant, SO_2 can modify the foliar symptoms caused by exposure of tomato to O_3 (11). Less is known about the effects of O_3 and SO_2 mixtures on vegetative growth and yield, particularly as the relative concentrations of the two pollutants are changed. There is a need to define tomato response to repeated exposures to O_3 + SO_2.

Possible effects of parasitic plant pathogens and air pollutants include: enhancement or suppression of parasitism and pathogenicity, enhancement or suppression of air pollutant effects, or no interaction of these factors. Although most data supporting parasite-pollutant interactions involve the enhancement or suppression of biotic foliar pathogens by pollutants, there is some evidence for interactions between root pathogens and air pollutants (6). For example, Fusarium wilt developed more slowly on 'Rutgers' tomato chronically exposed to low concentrations of O_3 than on those grown in charcoal-filtered air (12). Further evidence for interactions between air pollutants and root-infecting organisms was provided by Weber et al (20); reproduction of *Heterodera glycines* and *Paratrichodorus minor* was inhibited by exposure of the host, *Glycine max* (L.) Merr., to O_3 or SO_2. Reproduction of *Pratylenchus penetrans* (Cobb) Filipjev and Schuurmans-Stekhoven was stimulated on soybeans exposed to SO_2. The possible effects of root pathogens on plant response to air pollutants have not been extensively studied, and the potential for interaction between air pollutants and nematodes is unknown for most species including tomato.

The current study was initiated to examine tomato response to possible interactions between O_3 dose and nematode inoculum levels; to determine the influence of infection of tomato by *P. penetrans* on plant response to exposure to O_3 and SO_2 alone and in combination; and to characterize the interactions of O_3 and SO_2 dose and nematode populations.

MATERIALS AND METHODS

Plant culture. Tomato seeds (cultivar Walter) were germinated in vermiculite. Seedlings were transplanted to 15-cm-diameter clay pots containing pasteurized clay loam soil and 0.17-mm (mean particle size) sand (1:1, v/v) plus 160 g of dolomitic lime per cubic meter of soil mixture. Each plant was fertilized weekly with 100 ml of nutrient solution containing 700 g of VHPF (6-25-15 NPK fertilizer with micronutrients, Miller Chemical and Fertilizer Corp., Hanover, PA 17330), 123 g of KNO_3, and 227 g of $MgSO_4$ per 80 L applied at half strength beginning 1 wk after transplanting. After fruiting was initiated, nutrient was applied full strength as needed once or twice a week. Dimethoate was applied weekly at recommended rates for control of leaf miners. Beginning at flowering, a foliar spray of $Ca(NO_3)_2$ (4.4 g/ L) was applied weekly to prevent blossom end rot. Resmethrin (B. G. Pratt Div., Gabriel Chemicals LTD, Patterson, NJ 07509) was applied as needed to control whiteflies. Tomatoes were grown in a greenhouse with charcoal-filtered air. Supplemental lighting of 15 klux was provided during a 12-hr photoperiod. Day temperatures in the winter were 24 ± 3 C and night temperatures were 18 ± 3 C. The

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temperatures for the summer were ~30 ± 3 C and 23 ± 3 C for day and night, respectively.

Nematodes. Cultures of *P. penetrans* originally isolated from potato were maintained on soybeans in the greenhouse. Nematodes were extracted from soybean roots in a Seinhorst mist chamber (1). Plants were inoculated with a suspension containing the desired number of nematodes in tap water by pouring the suspension into holes punched into the soil with a pencil or cork borer near the base of each plant. Uninoculated plants were treated similarly with tap water.

Exposures to pollutants. Tomatoes were exposed for 3 or 4 hr to O_3, SO_2, $SO_2 + O_3$, or charcoal-filtered air in continuously stirred tank reactor (CSTR) chambers (10) in the greenhouse and were placed on greenhouse benches between exposures. Chamber temperatures during exposures were approximately 3 C greater than greenhouse temperatures. Ozone was generated by a Welsbach O_3 generator, and concentrations were monitored with a chemiluminescence O_3 analyzer (Monitor Labs, Inc., San Diego, CA 92121). Sulfur dioxide was provided from a tank containing 1% SO_2 and was monitored with a flame photometric SO_2 analyzer (Meloy Laboratories, Inc., Springfield, VA 22152). Each gas analyzer was calibrated by a portable Model 8500 Monitor Labs calibrator.

Evaluation of pollutant effects and nematode populations. When experiments were terminated, fruits were picked and weighed (including peduncles) separately from the vegetative shoots. Plants were harvested by cutting the stem at the soil surface to separate the roots and shoots. The vegetative shoots were weighed, oven-dried at 70 C, and reweighed. Soil and roots from each pot were placed in a plastic bag and stored at 13 C until soil or root assays were made for nematodes. Root systems were gently shaken to free them from soil, washed in a stream of tap water, blotted in paper toweling, and weighed. Roots were placed in a mist chamber for 12–16 days for extraction of nematodes, during which time nematodes were collected for counting. Five hundred grams of the soil from each pot was assayed for *P. penetrans* by using a semiautomatic elutriator and centrifugation-flotation (1). Root fragments in the soil were collected on a 425-μm sieve during elutriation and placed in a mist chamber for extraction of nematodes. Results of these nematode population assays were expressed on a per pot basis.

Data analysis. Data were analyzed by analysis of variance (ANOVA) (3). For O_3-dose experiments, best-fitting regression equations were obtained (14). For experiments involving factorial arrangement of *P. penetrans* (P), O_3, and SO_2 factors, the ANOVA model may be written as:

$$\hat{Y} = \hat{\mu} + \hat{\beta}_0 P + \hat{\beta}_1 O_3 + \hat{\beta}_2 SO_2 + \hat{\beta}_3(O_3 \times SO_2) + \hat{\beta}_4 (O_3 \times P) + \hat{\beta}_5 (SO_2 \times P) + \hat{\beta}_6((O_3 + SO_2) \times P),$$

in which $\hat{Y}$ is the predicted mean of the dependent variable (eg, shoot dry weight), $\hat{\mu}$ is the experimental mean, and $\hat{\beta}_i$, $i = 0, 1, 2 \ldots 6$ are the main or interaction effects involving P, O_3, and SO_2. The means and $\hat{\beta}_i$s were calculated from the data, and significance of the $\hat{\beta}_i$s was determined by single-degree-of-freedom F tests. Presence or absence of a factor (P, O_3, or SO_2) was designated by a +1 or −1, respectively (3).

RESULTS

Effects of O_3 dose on tomato plants inoculated with *P. penetrans*. Two experiments were done to determine the effects of various combinations of O_3 doses and initial nematode inoculum levels on pollutant × nematode interactions. In the first experiment, each of 16 tomato seedlings were inoculated with 500 *P. penetrans* 25 days after transplanting. Sixteen seedlings were treated similarly with water blanks. Inoculated and uninoculated plants were exposed to O_3 at 0.075, 0.15, 0.3, and 0.6 μl/L of air for 3 hr twice a week for 5 wk during December and January. In a second experiment begun in April, 48 tomato seedlings were each inoculated with 40 *P. penetrans* 12 days after transplanting. Sixteen additional seedlings treated with water blanks served as uninoculated controls. The following day, inoculated and uninoculated plants were exposed to 0, 0.1, 0.2, or 0.4 μl O_3 per liter of air for 3 hr. One day after exposure, additional nematodes were introduced into some of the pots already containing nematodes to give four initial nematode populations (P_i) of 0, 40, 400, or 4,000 nematodes per plant. Thus, the factorial experiment involved 4 P_is × 4 O_3 doses. Exposures continued twice a week for 5 wk. In both dose experiments, a split-plot design with four replications was used.

In both experiments, *P. penetrans* did not influence plant response to O_3 dose. *P. penetrans* also had little effect on tomato growth, regardless of P_i. For most variables (eg, shoot, leaf, and stem dry weight) measured in both experiments, the response of tomato growth to $\log_{10}$ O_3 concentration (in microliters per liter of air) was fit by a quadratic model. A typical result was given by the equation obtained for shoot dry weight ($\hat{Y}$) in the second experiment: $\hat{Y} = 15.51 + 8.83(\log_{10} O_3 \text{ concentration}) - 8.23(\log_{10} O_3 \text{ concentration})^2$ (Fig. 1). In this equation, a significant ($P = 0.05$) proportion of the variation in the experiment was due to the quadratic response of shoot dry weight to $\log_{10}$ O_3 concentration ($R^2 = 0.76$).

Effects of *P. penetrans* and equal doses of O_3 and SO_2 on tomato growth. Twelve days after being transplanted, tomato seedlings were inoculated with 2,000 nematodes per plant. Exposures to air pollutants were initiated 2 days after inoculation. Groups of inoculated and uninoculated tomato plants were exposed either to charcoal-filtered air, 0.2 μl O_3, 0.2 μl SO_2, or to 0.2 μl O_3 + 0.2 μl SO_2 per liter of air for 4 hr two times a week for 7.5 wk, a total of 15 exposures. The experimental design consisted of eight pollutant × nematode treatment combinations and five plants per experimental unit.

The graphic representation of the weights of the components of the vegetative shoot (Fig. 2A) and of the fruit (Fig. 3A) may be used to evaluate the magnitude of tomato response to the various treatments. More precise information about the relative importance of the factors examined may be gained through interpretation of their main and interaction effects in an ANOVA model (Table 1). Results were interpreted in terms of these effects. Treatments containing O_3 inhibited leaf, stem, and shoot growth

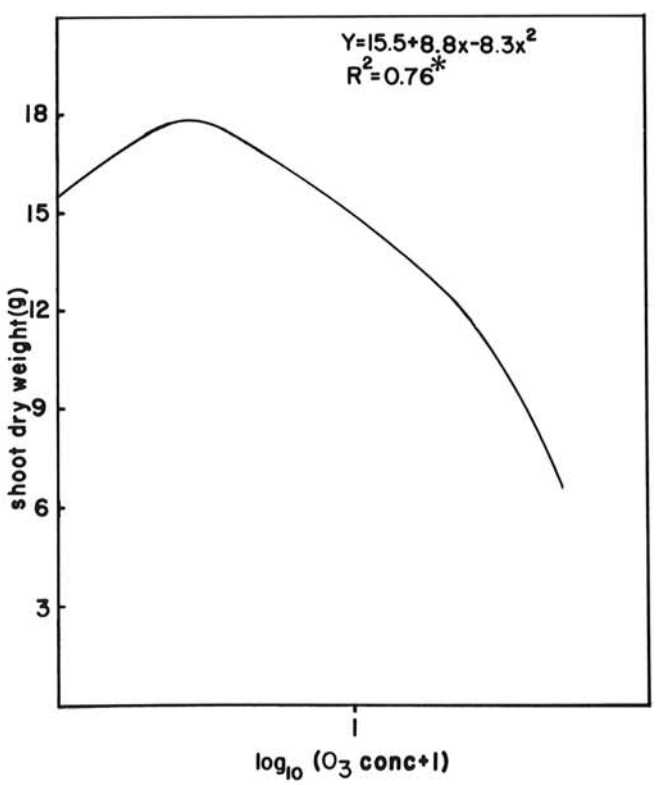

Fig. 1. Fitted regression equation of shoot dry weight to $\log_{10} O_3$ dose in experiment 2.

(dry weight). The smaller (but significant) negative values for the SO_2 effect indicate that SO_2 moderately suppressed plant growth. O_3 and SO_2 acted additively in suppression of total fruit growth, but the negative $O_3 \times SO_2$ effect on weight of the largest fruit was greater than predicted by addition of the O_3 and SO_2 main effects.

Because values for $\hat{\beta}_0$ (*P. penetrans* effect) were always small and nonsignificant, they are not given in Tables 1 and 2. Although there was no significant main effect of the nematode factor, pollutant × nematode interactions did occur. Stem and shoot growth of tomato plants inoculated with *P. penetrans* were generally less affected by $O_3 + SO_2$ treatment than was growth of uninoculated plants (Table 1). Similarly, weight of the largest fruit of O_3-exposed plants was dependent on nematode treatment; fruits on inoculated plants were larger. Air pollutants did not affect final numbers of nematodes (P_f) in this experiment ($P = 0.05$).

Response of tomato to *P. penetrans* and 0.2 μl O_3 and 0.8 μl SO_2 per liter of air. The effects of 3-hr exposure to 0.2 μl O_3 alone and in combination with 0.8 μl SO_2 per liter of air were examined in a second experiment. Tomatoes were inoculated with 2,000 nematodes per pot 16 days after transplanting, and exposures began 1 day after inoculation. Plants were exposed twice a week (a total of 15 exposures) during an 8-wk period. A split-plot design with eight pollutant × nematode treatment combinations and eight replications was used in this experiment.

Mean dry weights (grams) of the components of tomato vegetative shoot growth are presented for the pollutant and nematode treatments in Fig. 2B, and fresh weights of fruit are represented in Fig. 3B. Interpretations are based on main and interaction effects (Table 2). Sulfur dioxide at 0.8 μl/L of air caused severe foliar injury of tomato after 15 exposures, resulting in suppressed vegetative growth (dry weight, Table 2). The large negative impact of SO_2 on growth in this experiment accounted for much more of the pollutant main effects than did O_3. This is shown by the respective values for leaf, stem, axillary, and shoot dry weight. Sulfur dioxide also negatively affected fruit growth. When O_3 and SO_2 were present together, they acted antagonistically. The significant positive values for the $O_3 \times SO_2$ effect indicate that mixtures of O_3 and SO_2 caused less damage than could be predicted from the main effects of these pollutants.

The presence of *P. penetrans* enhanced the negative effect of $O_3 + SO_2$ on leaf growth (dry weight, Table 2) but suppressed the $O_3 + SO_2$ effect on axillary shoot production. Nematodes did not affect

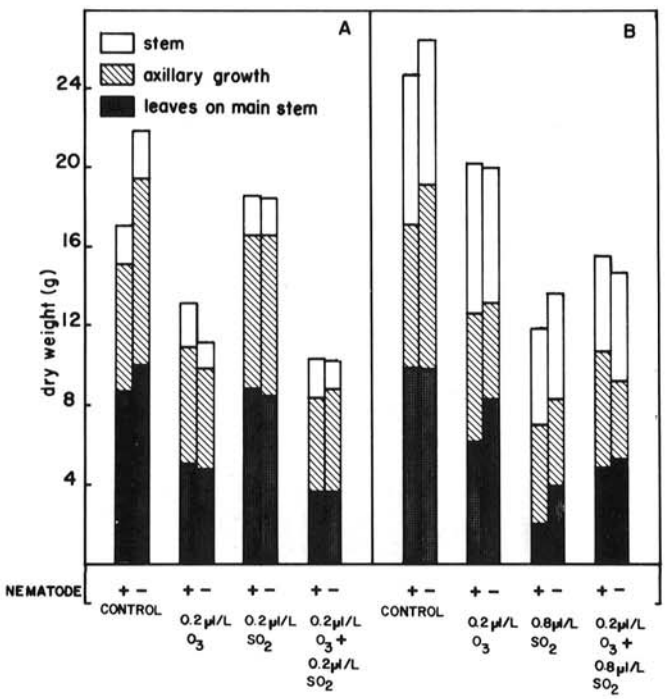

Fig. 2. Relationships between shoot dry weights of tomato plants exposed to air pollutants and either inoculated or uninoculated with *Pratylenchus penetrans*. **A,** Plants exposed to 0.2 μl O_3, 0.2 μl SO_2 per liter of air, those concentrations of $O_3 + SO_2$ combined, or charcoal-filtered air (control). **B,** Plants exposed to 0.2 μl O_3, 0.8 μl SO_2 per liter of air, $O_3 + SO_2$, or charcoal-filtered air.

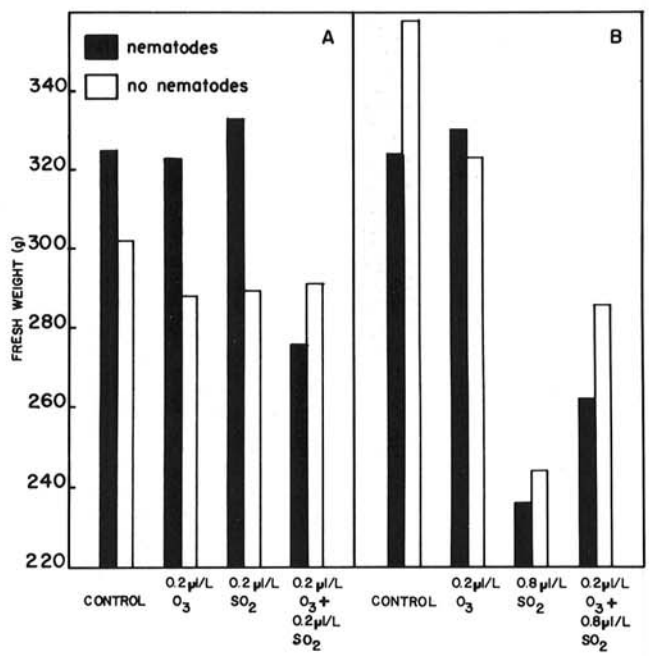

Fig. 3. Fresh weights of tomato fruits of plants exposed to O_3 and SO_2 in the presence or absence of *Pratylenchus penetrans*. **A,** Plants exposed to 0.2 μl O_3, 0.2 μl SO_2 per liter of air, those concentrations of $O_3 + SO_2$ combined, or charcoal-filtered air (control). **B,** Plants exposed to 0.2 μl O_3, 0.8 μl SO_2 per liter of air, $O_3 + SO_2$, or charcoal-filtered air.

TABLE 1. Influence of 0.2 μl/L O_3, 0.2 μl/L SO_2 and *Pratylenchus penetrans* on growth of tomato plants[a]

Dependent variable ($\hat{Y}$)	Main and interaction effects (g)							
	$\hat{\mu}$[b]	O_3	SO_2	$O_3 \times SO_2$	$O_3 \times$ *P. penetrans*	$SO_2 \times$ *P. penetrans*	$O_3 \times SO_2 \times$ *P. penetrans*	± S. E. (effect)
Dry weight (g)								
Leaf	6.57	−4.62**	−0.80*	−0.13	−0.37	−0.29	0.55	0.42
Stem	6.76	−3.10**	−0.65*	−0.12	−0.60	−0.16	0.70*	0.30
Axillary	1.86	−0.34	0.18	0.03	−0.50	−0.02	0.25	0.17
Shoot	15.19	−8.06**	−1.62*	−0.22	−1.48	−0.46	1.50*	0.77
Fresh weight (g)								
Largest fruit	119.3	1.2	−1.7	−21.8*	19.5*	−5.8	10.4	4.2
Fruit (total)	303.6	−17.9	−12.3	−9.54	12.1	7.3	17.4	6.8

[a] Plants were exposed to O_3, SO_2, or $O_3 + SO_2$ for 4 hr two times a week for 8 wk. Plants were inoculated with 2,000 nematodes per pot. Significance of main and interaction effects are $P = 0.05$(*) and $P = 0.01$(**).

[b] $\hat{\mu}$ = experimental mean.

TABLE 2. Influence of 0.2 μl/L O_3 and 0.8 μl/L SO_2 and *Pratylenchus penetrans* on growth of tomato plants[a]

Dependent variable ($\hat{Y}$)	$\hat{\mu}$[b] (g)	Main and interaction effects (g)						
		O_3	SO_2	$O_3 \times SO_2$	$O_3 \times$ *P. penetrans*	$SO_2 \times$ *P. penetrans*	$O_3 \times SO_2 \times$ *P. penetrans*	± S. E. (effect)
Dry weight (g)								
Leaf	6.95	−0.47	−4.78**	2.02**	−0.09	−0.24	−1.22**	0.42
Stem	6.46	−0.35	−2.27**	0.32	0.11	0.13	−0.38	0.19
Axillary	6.38	−0.65	−1.88**	1.59*	−1.08	0.08	1.46*	0.37
Shoot	19.79	−1.47**	−8.93**	3.94*	−1.06	−0.02	−0.12	0.76
Fresh weight (g)								
Fruit (total)	307	10	−77**	25**	−6	2	14	6.6

[a] Plants were exposed to O_3, SO_2, or $O_3 + SO_2$ 3 hr two times a week for 8 wk. Plants were inoculated with 2,000 nematodes per pot. Significant main and interaction effects were $P = 0.05$(*) and $P = 0.01$(**).
[b] $\hat{\mu}$ = Experimental mean.

overall shoot or fruit response to treatment with $O_3 + SO_2$. Ozone at 0.2 μl + 0.8 μl SO_2 per liter of air caused an average increase of 2,000 nematodes per pot over the experimental mean of 5,300 nematodes ($P = 0.01$). No other changes in nematode populations were significant ($P = 0.05$).

DISCUSSION

Researchers have emphasized that the additive, synergistic, or antagonistic nature of plant response to pollutant mixtures at various concentrations depends on the plant species (19). Characterization of other factors influencing plant response to mixtures of $O_3 + SO_2$ has been difficult, perhaps because too great a reliance was placed on foliar injury as a measurement of pollutant interaction. Reinert et al (17) documented the major role of foliar injury evaluations in research on the effects of pollutant combinations. Reports of poor correlation between foliar injury and yield response of tomato to O_3 exposures indicated that visual evaluations of foliar injury were not an adequate measure of tomato response to O_3 exposure (15). Another difficulty in evaluating air pollutant interactions is the poorly understood influence of environmental variables on plant response. Reported differences in plant response to pollutant mixtures under different runs of the same exposure regime suggest that the magnitude of plant response to a given $O_3 + SO_2$ combination may be dependent on environmental conditions (18).

Comparison of the results of our third and fourth experiments has provided insight into the importance of the respective single-gas concentration in determining plant response to mixtures of $O_3 + SO_2$. Our results with O_3 at 0.2 μl and SO_2 at 0.2 μl per liter of air indicated that when SO_2 caused little growth suppression, pollutant interactions tended to be rare; the effects of 0.2 μl O_3 + 0.2 μl SO_2 per liter of air were additive. In contrast, our results with 0.2 μl O_3 and 0.8 μl SO_2 per liter of air indicated that when SO_2 severely inhibited plant growth, O_3 and SO_2 had interactive effects; less injury was caused by mixtures of O_3 and SO_2 than was predicted by addition of their respective main effects. Tomato response to mixtures of O_3 and SO_2, therefore, was dependent upon the effects of these pollutants at a given concentration.

Heagle and Johnston (8) reached similar conclusions based on work with soybean. Additive or synergistic effects were reported for mixtures of O_3 and SO_2 when each was present at relatively low concentrations (7), but antagonism occurred when more injurious levels of each gas were used (8). These relationships are likely to vary with plant species (6).

Nematodes altered tomato response to mixtures of O_3 and SO_2. Exposed plants 1–3 wk old inoculated with *P. penetrans* often developed more foliar injury than did uninoculated plants, but injury differences often could not be detected visually as exposures continued. Nevertheless, biomass measurements revealed the occurrence of variable pollutant × nematode interactions.

Nematodes suppressed the negative effects of 0.2 μl O_3 + 0.2 μl SO_2 per liter of air on stem and shoot dry weight of tomato. *P. penetrans* also suppressed the negative effect of 0.2 μl O_3 + 0.8 μl SO_2 per liter of air on axillary shoot growth, but at the same time enhanced foliar injury (lowered leaf dry weight). As in the case of the two-way interactions between O_3 and SO_2, it appeared that nematode × pollutant interactions were influenced by the single-gas concentrations. The absence of O_3-dose × *P. penetrans* interactions in the first and second experiments suggests that either the SO_2 dose or the ratio of O_3 concentration to SO_2 concentration was critical in $O_3 \times SO_2 \times$ *P. penetrans* interactions. Because *P. penetrans* did not greatly suppress tomato growth in any experiment, the potential for air pollutant × nematode interaction on plants severely stressed by this parasite is unknown.

Response of nematode populations to air pollutant treatments varied. Walter tomatoes had limited abilities to support large population densities of *P. penetrans* (ie, P_i = 4,000), especially when plants were severely stressed by air pollutants. Dolliver (4) reported that reproduction of *P. penetrans* was stimulated by treatments that suppressed shoot growth of *Pisum sativum* L. Subsequent findings have both supported (5,20) and contradicted (2) his conclusions. We found that the interaction of 0.2 μl O_3 and 0.8 μl SO_2 per liter of air (which suppressed shoot growth) enhanced reproduction of *P. penetrans* on tomato. We did not observe enhanced reproduction of *P. penetrans* in any other experiment, even when comparable levels of shoot growth suppression occurred. Therefore, it appeared that simple shoot growth suppression did not account for all treatment effects on nematode populations.

Plants respond to O_3 or SO_2 differently in the presence of pollutant mixtures or of root-infecting microorganisms, but these interactions are probably dosage- and environmentally-dependent. Air quality standards will not be adequately determined until the question of pollutant × pollutant and pollutant × parasite interaction is given greater priority.

LITERATURE CITED

1. Barker, K. R. (chairman). 1978. Determining nematode population responses to control agents. Pages 114–126 in: Methods for evaluating plant fungicides, nematocides, and bacteriocides. E. I. Zehr, ed. Am. Phytopathol. Soc., St. Paul, MN 141 pp.
2. Barker, K. R., Hussey, R. S., and Yang, H. 1975. Effects of light intensity and quality on reproduction of plant parasitic nematodes. J. Nematol. 7:364-368.
3. Cochran, W. G., and Cox, G. M. 1957. Experimental Designs. 2nd ed. John Wiley & Sons, New York. 611 pp.
4. Dolliver, J. S. 1961. Population levels of *Pratylenchus penetrans* as influenced by treatments affecting dry weights of Wando pea plants. Phytopathology 51:364-367.
5. Faulkner, L. T., and Skotland, C. B. 1965. Interactions of *Verticillium dahliae* and *Pratylenchus minyus* on Verticillium wilt of peppermint. Phytopathology 55:583-586.
6. Heagle, A. S. 1973. Interactions between air pollutants and plant parasites. Annu. Rev. Phytopathol. 11:365-388.
7. Heagle, A. S., Body, D. E., and Neely, G. E. 1974. Injury and yield responses of soybean to chronic doses of ozone and sulfur dioxide in the field. Phytopathology 64:132-136.
8. Heagle, A. S., and Johnston, J. W. 1979. Variable responses of soybeans to mixtures of ozone and sulfur dioxide. J. Air Pollut. Control Assoc. 29:729-732.
9. Heck, W. W. 1968. Factors influencing expression of oxidant damage

to plants. Annu. Rev. Phytopathol. 6:165-188.
10. Heck, W. W., Philbeck, R. B., and Dunning, J. A. 1978. A Continuous Stirred Tank Reactor (CSTR) System for Exposing Plants to Gaseous Air Contaminants: Principles, Specifications, Construction, and Operation. Agricultural Research Series No. 181, U.S. Govt. Printing Office, Washington, DC. 23 pp.
11. Hofstra, G., and Beckerson, D. W. 1980. Foliar response of five plant species to ozone and a sulphur dioxide mixture after a sulphur dioxide pre-exposure. Atmos. Environ. 15:383-389.
12. Manning, W. J., and Vardaro, P. M. 1976. Ozone and *Fusarium* effects on the growth and development of a wilt susceptible and a wilt resistant tomato. (Abstr.) Proc. Am. Phytopathol. Soc. 3:227.
13. Mudd, J. B. 1975. Sulfur dioxide. Pages 9–22 in: Responses of Plants to Air Pollution. J. B. Mudd and T. T. Kozlowski, eds. Academic Press, New York. 383 pp.
14. Neter, J., and Wasserman, W. 1974. Applied Linear Statistical Models. Richard D. Irwin, Inc., Homewood, IL. 842 pp.
15. Oshima, R. G., Braegelman, P. K., Baldwin, D. W., Vanway, V., and Taylor, O. C. 1977. Responses of five cultivars of fresh market tomato to ozone: a contrast of cultivar screening with foliar injury and yield. J. Am. Soc. Hortic. Sci. 102:286-289.
16. Reinert, R. A. 1980. Assessment of crop productivity after chronic exposures to ozone or pollutant combinations. Preprint 80-26.4. 73rd Annu. Mtg. Air Pollut. Control Assoc. 23 pp.
17. Reinert, R. A., Heagle, A. S., and Heck, W. W. 1975. Plant response to pollutant combinations. Pages 159–177 in: Responses of plants to air pollution. J. B. Mudd, and T. T. Kozlowski, eds. Academic Press, New York. 383 pp.
18. Tingey, D. T., Heck, W. W., and Reinert, R. A. 1971. Effect of low concentrations of ozone and sulfur dioxide on foliage, growth, and yield of radish. J. Am. Soc. Hortic. Sci. 96:369-371.
19. Tingey, D. T., Reinert, R. A., Dunning, J. A., and Heck, W. W. 1973. Foliar injury responses of eleven plant species to ozone/sulfur dioxide mixtures. Atmos. Environ. 7:201-208.
20. Weber, D. W., Reinert, R. A., and Barker, K. R. 1979. Influence of ozone and sulfur dioxide on the reproduction and host-parasitic relationships of selected plant parasitic nematodes. Phytopathology 69:624-628.