Influence of Mycorrhizae on the Growth of Loblolly Pine Seedlings Exposed to Ozone and Sulfur Dioxide

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ABSTRACT

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Loblolly pine seedlings, with and without ectomycorrhizae, were exposed to ozone (O_3) at 0.07 μl/L and sulfur dioxide (SO_2) at 0.06 μl/L, singly and in combination, 6 hr/day for 5 wk. Exposure to either pollutant alone neither affected mycorrhizal formation nor changed reducing sugar concentrations in the roots. Root growth of nonmycorrhizal seedlings was more severely inhibited by each fumigation treatment than was shoot growth, and the root:shoot ratio in these seedlings was lower than that of unfumigated seedlings. Mycorrhizae altered the pollutant effects on root and shoot growth and promoted root growth so that no pollution treatment effects were evident. Fumigated mycorrhizal seedlings had a higher root:shoot ratio compared to unfumigated mycorrhizal seedlings.

Ambient concentrations of ozone (O_3) and sulfur dioxide (SO_2) are known to affect the growth of pollutant-sensitive forest trees (1,6,21,24) and to induce alterations in processes involved with foliar gas exchange, CO_2 fixation, and photosynthate allocation (8,11,15,21,23). The effects of these pollutants on root growth and physiology are not well established; this is especially true regarding the mycorrhizal associations essential for seedling survival, general vigor, and productivity of many species. McCool et al (19) reported that chlamydospore production by *Glomus fasiculatus* (Thaxter) Gerd. & Trappe was decreased on roots of citrange exposed to O_3 at 1.0 μl/L for 4 hr. Moreover, endomycorrhizal formation was reduced after fumigation with O_3 at 0.9 μl/L for 6 hr once each week for 19 wk, and this O_3 dose also reduced height growth and biomass of mycorrhizal plants. Carney et al (4) and Garrett et al (7) measured O_2 uptake in mycorrhizal and nonmycorrhizal loblolly pine root segments exposed to 0.05 or 0.50 μl/L O_3 or SO_2 for 3 hr. They observed a greater reduction in O_2 uptake in nonmycorrhizal roots and suggested that ectomycorrhizae may, to some degree, protect plants from these gases.

These reports indicate that O_3 and SO_2 can affect root-fungus interactions in both ecto- and endomycorrhizal associations. However, the relationships between ectomycorrhizal development, pollutant stress, and seedling tree growth remain unclear. The objectives of our study were to examine the effects of low concentrations of O_3 and SO_2, singly and in combination, on mycorrhizal formation involving *Pisolithus tinctorius* (Pers.) Coker and Couch and loblolly pine (*Pinus taeda* L.) seedlings and on the relative differences in growth response of mycorrhizal and nonmycorrhizal seedlings.

MATERIALS AND METHODS

Loblolly pine seeds from the open pollinated half-sib family, 2-8, were obtained from the Virginia Division of Forestry, Providence Forge, VA. Stratified seeds were surface sterilized for 5 min in a 0.5% sodium hypochlorite solution, rinsed in tap water, and sown in a planting mix of Weblite (Weblite Corp. Inc., Roanoke, VA), hammermilled peatmoss, and grade-two vermiculite (2:1:1, v/v ratio). The planting mix was steam pasteurized for 1 hr and amended with 223 g/m^3 of 18-6-12 (N-P-K) Osmocote® fertilizer (Sierra Chemical Co., Milpitas, CA).

Two-week-old seedlings, used for mycorrhizal colonization studies, were transplanted into the growth medium infested with 12-wk-old mycelia of the ectomycorrhizal fungus, *P. tinctorius*. Inoculum was produced by the method of Marx and Bryan (16). The planting mix was infested by filling each cavity (615 cc) of a Wellair plug-type container (Wiesinger Systems Ltd., Winnipeg, Canada) with 350 cc of planting mix over which a layer of 50–60 cc of inoculum of *P. tinctorius* was spread. Planting mix was added over the fungus-infested layer, and one seedling per cavity (20 per Wellair container) was transplanted into the mix above the inoculum band to ensure that roots would grow through the inoculum. For root carbohydrate analysis, 2-wk-old seedlings were transplanted into uninfested growth medium.

After transplanting, both groups of seedlings were maintained in a greenhouse supplied with charcoal-filtered air and day/night environmental conditions of 27/20 ± 4 C and 60/80 ± 15% RH. The seedlings received supplemental lighting of 500–600 μmol/m^2/sec photon flux density to maintain a 14-hr photoperiod.

Fumigation of the pine seedlings began in April when seedlings were approximately 3 wk old, and the experiment was repeated 1 mo later. Seedlings were fumigated 6 hr each day (from 0800 hours to 1400 hours) for 35 consecutive days in four continuously stirred tank reactors (11). Pollutant treatments included: charcoal-filtered air (control), O_3 at 0.07 μl/L, SO_2 at 0.06 μl/L, and O_3 at 0.07 μl/L plus SO_2 at 0.06 μl/L. Initially, and again after 17 days of exposure, treatments were randomly assigned to different continuously stirred tank reactors to minimize any chamber effect. Relative humidity within the chambers was maintained at 65 ± 5%, and temperature was maintained at 29 ± 1 C. Photon flux density was 400 ± 20 μmol/m^2/sec.

Ozone was generated with a model T-408 Welsbach Laboratory Ozonator (Welsbach Ozone Systems Corp., Philadelphia, PA) and monitored with a Bendix model 8002 Chemiluminescent Ozone Analyzer (Bendix Process Instruments Div., Lewisburg, WV). The

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O_3 analyzer was calibrated with a Photocal model 3000 Automated Ozone Calibration System (Columbia Scientific Industries, Austin, TX). Sulfur dioxide was dispensed from commercial, high-pressure, bottled SO_2 diluted in nitrogen (1.03% SO_2) and was monitored with a model 43 Pulsed Fluorescent Abient Sulfur Dioxide Analyzer (Thermo Electron Corp., Hopkinton, MA) which was calibrated with a Bendix Dynamic Calibration System utilizing an SO_2 permeation tube.

Total reducing and nonreducing sugar concentrations of mycorrhizal-free loblolly seedling roots were determined with a Technicon Auto Analyzer (Technicon Instrument Corp., Tarrytown, NY) by utilizing the reaction of reducing sugars with *p*-hydroxybenzoic acid hydrazide (5). Sugars were extracted from 100 mg of ground root tissue for 1 hr in hot H_2O and in hot H_2O plus 0.02 N H_2SO_4. Nonreducing sugar concentrations were calculated as the difference between samples processed with the two extraction procedures.

The number of short roots and percentage of roots with mycorrhizae was determined by adapting the modified line-intersect method developed by Tennant (26) to estimate root length. This method was determined to have an error of $\leqslant 3.6\%$ when compared to counting all mycorrhizal root tips. Both monopodial and bifurcate mycorrhizal tips were counted. A random sample of mycorrhizal roots was fixed in formalin, acetic acid, and alcohol, embedded in paraffin, stained with saffranin and fast green, sectioned, and viewed microscopically to determine the presence of a Hartig Net and a fungal mantle.

Every 7 days, beginning with the first day of fumigation, seedling height was measured to the nearest millimeter. Measurements were made from the cotylendonary node to the tips of the longest needles. At the end of the fifth week, seedlings were removed from the Wellair containers, washed in tap water, and separated into shoots and roots. They were then oven-dried at 80 C for 24 hr and weighed.

The experimental design used to examine pollutant effects on short-root growth, mycorrhizal development, and root sugar concentrations was a simple one-way analysis of variance. The main treatment effect was pollutant type and means were separated by Duncan's multiple range test, $P = 0.05$. The general experimental design used to investigate the effects of pollutants and mycorrhizal associations on seedling growth components consisted of an unbalanced split-plot with two replications over time (blocks). Whole plot treatments were gaseous pollutants, with one pollutant treatment per continuously stirred tank reactor, and time. The subplot treatment was the mycorrhizal status of the seedlings. Root sampling procedures differed between mycorrhizal and nonmycorrhizal seedlings since root material from these two treatments were used for different experimental measurements. Therefore, total dry weight and root dry weight data for mycorrhizal and nonmycorrhizal treatments were analyzed separately by one-way analysis of variance, and Duncan's multiple range test was used to separate means.

Initial analysis of the split-plot model for shoot dry weight and weekly cumulative height growth indicated numerous interactions between mycorrhizal treatments, time, and pollutant exposures. Consequently, analyses of variance of these data were performed separately for mycorrhizal and nonmycorrhizal treatments and data from the two replicates over time were combined. Mycorrhizal and nonmycorrhizal treatments were compared within pollutant treatments by an unbalanced *t*-test. Variation in sample size between mycorrhizal and nonmycorrhizal seedlings reflected additional nonmycorrhizal root material used for carbohydrate analysis, the limited amount of fungal material available to produce mycorrhizal plants, and seedling mortality prior to pollutant exposures.

Height increases were measured on 40 nonmycorrhizal seedlings and 30 mycorrhizal seedlings per pollutant treatment. Root and shoot dry weights were determined on 60 nonmycorrhizal and 30 mycorrhizal seedlings per treatment. Nonmycorrhizal roots were bulked into 15 samples of four roots each for weight measurements because of the generally smaller root size in this treatment, whereas mycorrhizal roots were weighed individually. Numbers of short roots and percent mycorrhizal colonization were determined on 25 mycorrhizal seedlings per pollutant treatment. Reducing and nonreducing sugar contents of roots were measured in 20 nonmycorrhizal seedlings per pollutant treatment, bulked into five samples containing four root systems each.

RESULTS

Mycorrhizal formation in inoculated loblolly pine seedlings was extensive with nearly 70% of all short roots being mycorrhizal (Table 1). Both monopodial and bifurcate forms were evident, and a mantle of mycelium of *P. tinctorius* was visible with a dissecting microscope in most cases. Histological examination of mycorrhizal roots revealed a well-developed Hartig Net and mantle. Uninoculated seedlings were not mycorrhizal.

Mycorrhizal formation was not affected by a 5-wk exposure to any pollutant treatment. However, the number of short roots in mycorrhizal plants exposed to O_3 plus SO_2 was significantly fewer compared to unfumigated plants (Table 1). Reducing sugar concentrations in the roots of seedlings fumigated with O_3 plus SO_2 were 25% greater than in control plants. Other pollutant treatments did not affect reducing sugar content of the root. The O_3 and O_3 plus SO_2 exposures resulted in fivefold and threefold, respectively, increases in nonreducing sugar concentrations of the roots compared to unfumigated seedlings. No relationship between the concentration of reducing or nonreducing sugars and colonization by *P. tinctorius* was evident.

Shoot biomass was significantly affected by pollutant treatments in mycorrhizal seedlings (Table 2). All pollutant exposures decreased shoot dry weight by approximately 12% relative to control plants and no differences among treatments occurred. Visible foliar injury was not observed in any treatment. Pollutant exposure did not affect root dry weight in mycorrhizal seedlings, but it caused substantial changes in the root:shoot ratio. Fumigation with O_3, SO_2, and O_3 plus SO_2 resulted in increased root biomass relative to shoot biomass of 22, 13, and 13%, respectively, compared to control plants.

In nonmycorrhizal seedlings, O_3 alone and combined with SO_2 exposure resulted in significant decreases in shoot biomass of 10 and 13%, respectively, compared to control plants (Table 2). The relative reduction in shoot dry weight differed among pollutant treatments, an effect not observed in mycorrhizal seedlings. Sulfur dioxide exposure was least harmful, and O_3 plus SO_2 was most detrimental to shoot growth.

Root biomass production was adversely affected by pollutant exposure in nonmycorrhizal seedlings in contrast to mycorrhizal seedlings in which pollutants did not affect root dry weight. Ozone and SO_2 alone decreased root biomass by approximately 22% compared to controls, whereas the O_3 plus SO_2 treatment decreased root dry weight by 35%. The root:shoot ratio was also altered in fumigated nonmycorrhizal seedlings. Shoot growth was enhanced over root growth and this effect was opposite of that observed in pollutant-stressed mycorrhizal seedlings (Table 2).

Fumigation of nonmycorrhizal plants with O_3, SO_2, or O_3 plus SO_2 resulted in 14, 16, and 25%, respectively, increases in shoot biomass relative to root biomass. In fumigated seedlings, mycorrhizae enhanced root growth relative to shoot growth by 23–31% compared to nonmycorrhizal plants. The greatest effect of mycorrhizae occurred in the combined exposure to O_3 plus SO_2 after which shoot and root dry weight differed by 20 and 45%, respectively, between mycorrhizal and nonmycorrhizal seedlings.

An unbalanced *t*-test analysis of mycorrhizal and nonmycorrhizal seedling shoot dry weight within pollutant treatments indicated that mycorrhizae significantly ($P = 0.01$) enhanced shoot biomass accumulation in all instances. A folded *f*-test verified ($P = 0.01$) that variances between mycorrhizal and nonmycorrhizal seedlings were equal within each pollutant exposure regime. In the control treatment (no pollutants), mycorrhizae increased mean shoot dry weight by 19% relative to nonmycorrhizal seedlings (Table 2). Similar increases in shoot dry weight resulting from the mycorrhizal association in the O_3, SO_2, and O_3 plus SO_2 treatments were 17, 12, and 20%, respectively.

Weekly cumulative height growth of mycorrhizal seedlings was only slightly affected by pollutant exposure (Table 3). Ozone and O_3 plus SO_2 reduced height growth during the fourth week of fumigation; this effect was not evident at the end of 5 wk. In nonmycorrhizal seedlings, SO_2 exposure stimulated seedling height growth beginning at week 3 of the fumigation period. At week 5, height of SO_2-treated seedlings was approximately 10% greater than seedlings exposed to only charcoal-filtered air. No other consistant pollutant effects on seedling height growth occurred.

A *t*-test comparison of seedling height within pollutant treatments × week indicated numerous significant differences between mycorrhizal and nonmycorrhizal seedlings. In the control treatment, seedling height was significantly greater ($P = 0.01$) in mycorrhizal plants compared to uninoculated seedlings beginning with week 3 and continuing through the fumigation period (Table 3). Similar results were observed with the O_3 treatment except that significant differences ($P = 0.05$) in height growth initially occurred at week 4. In the SO_2 treatment, nonmycorrhizal seedling height increase was greater ($P = 0.05$) compared to mycorrhizal seedlings during the first week of fumigation. By week 2 of the pollutant exposure period, this effect was no longer observed.

DISCUSSION

Low concentrations of O_3 and/or SO_2 did not affect root colonization of loblolly pine seedlings by the ectomycorrhizal fungus, *P. tinctorius*. Although exposure to O_3 and SO_2 combined increased reducing and nonreducing sugar concentrations in roots, mycorrhizal formation was not enhanced. Bjorkman (2) and Marx et al (17) have reported that high soluble sugar concentrations in roots favor mycorrhizal colonization. In our experiments, the 25% increase in soluble carbohydrates in the combined pollutant treatment may have been insufficient to significantly affect mycorrhizal development since sugar concentrations in roots were not depleted in any of the other treatments. In contrast to our results, Jensen (12) observed that O_3 exposure (0.5 μl/L) significantly reduced soluble root carbohydrate in green ash seedlings. McCool and Menge (18) reported a reduction in reducing sugars in roots and colonization of tomato seedlings by the vesicular-arbuscular mycorrhizal fungus, *Glomus fasiculatus*, when plants were exposed to 0.15 or 0.30 μl/L O_3 for 3 hr twice weekly for 9 wk. An O_3 concentration higher than that used in our study appears necessary to significantly lower root carbohydrate content and thereby affect subsequent mycorrhizal colonization.

The presence of mycorrhizae substantially altered the growth response of loblolly pine to O_3 and SO_2 fumigation compared to nonmycorrhizal plants, and these effects were most evident on root growth. The greater shoot growth relative to root growth in pollutant-stressed nonmycorrhizal seedlings, compared to control plants, was expected since both O_3 and SO_2 are known to reduce translocation of photosynthate from leaves in a number of plant species (13,20,21,23). Reduced photosynthesis, interference with translocation processes, and increased leaf sink strength (injury repair and maintenance of homeostasis) may all be involved in retaining photosynthate within the foliage (13,20,23). The greater root growth relative to shoot growth in fumigated mycorrhizal seedlings, compared to control plants and fumigated nonmycorrhizal plants, suggests that *P. tinctorius* is capable of significantly modifying the root sink strength and apparently increasing root demand for photosynthate. This increase in root sink strength was sufficient to overcome the pollutant effect(s) on the foliar sink and supports the hypothesis of Handly and Sander (9) and Mayer (22) that mycorrhizal development promotes increased translocation of assimilates to the roots.

Mycorrhizae are known to aid in the adsorption and uptake of water and nutrient ions. They are especially important where movement of relatively immobile ions, such as phosphate, zinc, copper, and molybdenum to the root surface is a limiting factor (25). While the differences in biomass accumulation between roots and shoots in mycorrhizal and nonmycorrhizal seedlings exposed to O_3 and SO_2 must involve changes in photosynthate utilization, the effect of nutrient balances on altered growth patterns can be an important factor mediating this response. Calcium deficiencies have been reported to intensify O_3 symptom expression in tobacco (27) and foliar ATP concentrations were reduced in lodgepole-jackpine hybrids exposed to SO_2 (10). Further research investigating the physiological mechanism(s) by which mycorrhizae can alter plant

TABLE 1. Short roots, mycorrhizal formation, and soluble root carbohydrate contents of loblolly pine seedlings fumigated[w] for 5 wk with O_3 and SO_2 singly and in combination

Fumigation treatment	Short roots (no.)[x]	Mycorrhizal roots (%)[x]	Reducing[y] sugars	Non-reducing[y] sugars
Control	80.6 a[z]	67.4 a	17.3 b	0.5 b
O_3	81.3 a	67.7 a	15.1 b	2.3 a
SO_2	79.9 a	66.9 a	19.0 b	0.6 b
$O_3 + SO_2$	62.5 b	69.4 a	23.2 a	1.6 a

[w] O_3 at 0.07 μl/L and SO_2 at 0.06 μl/L.
[x] Numbers of short roots and percentages of roots with mycorrhizae per plant were determined by utilizing the line intersect method. Values are means of 25 plants per treatment.
[y] Values are expressed as milligrams per gram of root dry weight and are means of 20 plants per treatment.
[z] Means within the same column followed by the same letter are not significantly different ($P = 0.01$) according to Duncan's multiple range test.

TABLE 2. Dry weight of mycorrhizal and nonmycorrhizal loblolly pine seedlings fumigated[w] for 5 wk with O_3 and SO_2 singly and in combination

Root condition and fumigation treatment	Shoot[x] (mg)	Root[x] (mg)	R/S[y]
Mycorrhizal			
Control	212.4 a[z]	44.2 a	0.208
O_3	188.8 b	50.4 a	0.267
SO_2	188.5 b	44.8 a	0.238
$O_3 + SO_2$	186.9 b	44.8 a	0.240
Nonmycorrhizal			
Control	172.4 a	38.1 a	0.221
O_3	156.7 bc	29.7 b	0.190
SO_2	165.8 ab	30.7 b	0.185
$O_3 + SO_2$	150.6 c	24.8 c	0.165

[w] O_3 at 0.07 μl/L and SO_2 at 0.06 μl/L.
[x] Values are means of 30 mycorrhizal and 60 nonmycorrhizal seedlings per treatment.
[y] Root-to-shoot ratio.
[z] Means within mycorrhizal and nonmycorrhizal seedling groups and within columns followed by the same letter are not significantly different ($P = 0.05$) according to Duncan's multiple range test.

TABLE 3. Cumulative growth of mycorrhizal and nonmycorrhizal loblolly pine seedlings fumigated[x] with O_3 and SO_2 singly and in combination[z]

Root condition and fumigation treatment	Mean seedling height (mm)[y] at week: 1	2	3	4	5
Mycorrhizal					
Control	9.2 a[z]	25.0 a	37.3 a	52.1 a	63.3 a
O_3	7.3 a	24.1 a	35.1 a	48.4 b	61.4 a
SO_2	8.1 a	24.2 a	37.0 a	51.3 ab	62.5 a
$O_3 + SO_2$	7.5 a	22.4 a	35.4 a	48.3 b	59.4 a
Nonmycorrhizal					
Control	10.0 a	25.4 a	33.9 b	47.1 b	58.0 b
O_3	9.7 a	24.7 ab	33.7 b	45.5 b	57.2 b
SO_2	11.1 a	26.2 ab	37.7 a	51.3 a	63.2 a
$O_3 + SO_2$	9.6 a	23.1 b	32.8 b	46.1 b	57.6 b

[x] O_3 at 0.07 μl/L and SO_2 at 0.06 μl/L.
[y] Values are means of 30 mycorrhizal and 40 nonmycorrhizal seedlings per treatment.
[z] Means within weeks and mycorrhizal treatment followed by the same letter are not significantly different ($P = 0.05$) according to Duncan's multiple range test.

response to gaseous pollutants should consider the nutrient status of both the growth medium and the plant tissue.

Beneficial effects of mycorrhizae in ameliorting air pollutant stress have been reported in soybeans colonized by the endomycorrhizal fungus, *G. geosporum* (3), and in loblolly pine roots colonized by the ectomycorrhizal fungi, *P. tinctorius* and *Thelephora terrestris* (4,7). Results from our study support the findings of others (3,4,7) that mycorrhizae can protect plants against air pollution concentrations that typically occur in the ambient atmosphere. With loblolly pine seedlings, this effect was most pronounced on root development when biomass was twice as great in mycorrhizal plants compared to nonmycorrhizal plants fumigated with O_3 plus SO_2. The half-sib family, 2-8, that was used in this study is O_3 sensitive (14), and further research is necessary to examine the extent of mycorrhizal protection against air pollutants in O_3-insensitive and O_3-moderately sensitive loblolly pine families.

In our study, neither a fertilizer effect on shoot height growth resulting from SO_2 exposure nor an additive inhibition of shoot and root growth due to O_3 plus SO_2 fumigation occurred in mycorrhizal seedlings. However, both of these effects were observed in nonmycorrhizal seedlings. Additional research is required to determine the generality of protection from pollutant stress afforded by mycorrhizae. However, since most trees in native habitats are mycorrhizal, extrapolation of laboratory results obtained from plants lacking mycorrhizal associations to a field situation could lead to erroneous conclusions regarding the effects of air pollutant stress on seedling tree growth.

LITERATURE CITED

1. Benoit, L. F., Skelly, J. M., Moore, L. D., and Dochinger, L. S. 1982. Radial growth reductions of *Pinus strobus* L. correlated with foliar ozone sensitivity as an indicator of ozone-induced losses in eastern forests. Can. J. For. Res. 12:673-678.
2. Bjorkman, E. 1970. Mycorrhiza and tree nutrition in poor forest soils. Stud. For. Suec. 83:1-22.
3. Brewer, P. F., and Heagle, A. S. 1983. Interactions between *Glomus geosporum* and exposure of soybeans to ozone or simulated acid rain in the field. Phytopathology 73:1035-1040.
4. Carney, J. L., Garrett, H. E., and Hedrick, H. G. 1978. Influence of air pollution gases on oxygen uptake of pine roots with selected ectomycorrhizae. Phytopathology 68:1160-1163.
5. Davis, R. E. 1976. A combined automated procedure for the determination of reducing sugars and nicotine alkaloids in tobacco using a new reducing sugar method. Tob. Sci. 20:146-151.
6. Duchelle, S. F., Skelly, J. M., and Chevone, B. I. 1982. Oxidant effects on forest tree seedlings in the Appalachian Mountains. Water Air Soil Pollut. 18:363-375.
7. Garrett, H. E., Carney, J. L., and Hedrick, H. G. 1982. The effects of ozone and sulfur dioxide on respiration of ectomycorrhizal fungi. Can. J. For. Res. 12:141-145.
8. Hällgren, J. E., Linder, S., Richter, A., Troeng, E., and Granat, L. 1982. Uptake of SO_2 in shoots of Scots pine: Field measurements of net flux of sulphur in relation to stromatal conductance. Plant Cell Environ. 5:75-83.
9. Handley, W. R. C., and Sanders, C. I. 1962. The concentration of easily soluble reducing substances in roots and the formation of ectotrophic mycorrhizal associations. A re-examination of Bjorkman's hypothesis. Plant Soil 16:42-61.
10. Harvey, G. W., and Leggs, A. H. 1979. The effect of sulfur dioxide upon the metabolic level of adenosine triphosphate. Can. J. Bot. 57:759-764.
11. 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 181. U.S. Government Printing Office. Washington, DC. 32 pp.
12. Jensen, K. F. 1981. Ozone fumigation decreased the root carbohydrate content and dry weight of green ash seedlings. Environ. Pollut. 26:147-152.
13. Jones, T., and Mansfield, T. A. 1982. Studies on dry matter partitioning and distribution of ^{14}C-labeled assimilates in plants of *Phleum pratense* exposed to SO_2 pollution. Environ. Pollut. 28:199-207.
14. Kress, L. W., Skelly, J. M., and Hinkelmann, K. H. 1982. Relative sensitivity of 18 full-sib families of *Pinus taeda* to O_3. Can. J. For. Res. 12:202-209.
15. Mann, L. K., McLaughlin, S. B., and Shriner, D. S. 1980. Seasonal physiological responses of white pine under chronic air pollution stress. Environ. Exp. Bot. 20:99-105.
16. Marx, D. H., and Bryan, W. C. 1975. Growth and ectomycorrhizal development of loblolly pine seedlings in fumigated soil infested with the fungal symbiont *Pisolithus tinctorius*. For. Sci. 21:245-254.
17. Marx, D. H., Hatch, A. B., and Mendicino, J. F. 1977. High soil fertility decreases sucrose content and susceptibility of loblolly pine roots to ectomycorrhizal infection by *Pisolithus tinctorius*. Can. J. Bot. 5:1569-1574.
18. McCool, P. M., and Menge, J. A. 1983. Influence of ozone on carbon partitioning in tomato: Potential role of carbon flow in regulation of the mycorrhizal symbiosis under conditions of stress. New Phytol. 94:241-247.
19. McCool, P. M., Menge, J. A., and Taylor, O. C. 1979. Effects of ozone and HCl gas on the development of the mycorrhizal fungus *Glomus fasciculatus* and growth of Troyer citrange. J. Am. Soc. Hortic. Sci. 104:151-154.
20. McLaughlin, S. B., and McConathy, R. K. 1983. Effects of SO_2 and O_3 on allocation of ^{14}C-labeled photosynthate in *Phaseolus vulgaris*. Plant Physiol. 73:630-635.
21. McLaughlin, S. B., McConathy, R. K., Duvick, D., and Mann, K. L. 1981. Effects of chronic air pollution stress on photosynthesis, carbon allocation, and growth of white pine trees. For. Sci. 28:60-70.
22. Meyer, F. H. 1962. Der Buchen-und fichternmykorshija in verschiedenen Bodentypen, irhe, Beeinflussung durch Mineraldunger sowie fur die Mykorrhiza bildung wichtige faktoren. Mitt. Bundesforschungsanst. Forst Holzwirthsch. 54:1-73.
23. Noyes, R. D. 1980. The comparative effects of sulfur dioxide on photosynthesis and translocation in bean. Physiol. Plant Pathol. 16:73-79.
24. Phillips, S. O., Skelly, J. M., and Buckhart, H. E. 1977. Growth fluctuations of loblolly pine due to periodic air pollution levels: Interaction of rainfall and age. Phytopathology 67:716-720.
25. Ruehle, J. L., and Marx, D. H. 1979. Fiber, food, fuel, and fungal symbionts. Science 206:419-422.
26. Tennant, D. 1975. A test of a modified line-intersect method of estimating root length. J. Ecol. 63:994-1001.
27. Trevathan, L. E., and Moore, L. D. 1981. A study of calcium fertilization on weather fleck and chemical composition of flue-cured tobacco. Tobacco Sci. 25:102-105.