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Effects of Ozone and Acidic Deposition on Carbon Allocation and Mycorrhizal Colonization of *Pinus taeda* L. Seedlings

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ABSTRACT. Patterns of carbon allocation and mycorrhizal colonization were examined in loblolly pine seedlings from two half-sib families exposed to three ozone treatments (charcoal-filtered air, ambient air + 80 ppb O_3, and ambient air + 160 ppb O_3) and three rain pH levels (5.2, 4.5, and 3.3) for 12 weeks in open-topped chambers in a field setting. No statistically significant effects of ozone or rain pH were detected on biomass, root:shoot ratios, or carbon allocation; some consistent patterns were observed, however. Coarse root starch concentrations and mycorrhizal infection varied significantly with ozone levels. No significant interactions of ozone, rain pH, or genotype were detected. FOR. SCI. 37(1):5–16.

ADDITIONAL KEY WORDS. Starch, rhizosphere, air pollution.

MUCH OF THE RECENT AIR-POLLUTION-EFFECTS RESEARCH with plants has been concerned with impacts on aboveground growth and processes. The belowground component has been largely ignored, particularly for trees (McLaughlin 1985). There is a pressing need to examine the impacts of regional air pollutants, particularly ozone, on rhizosphere processes and associations, as a step toward understanding effects at the whole-plant level.

Blum and Tingey (1977) considered the alternative ways in which O_3 could influence the rhizosphere and concluded that direct effects of O_3 on the soil were not likely, but would be mediated by effects on aboveground components. Diminished photosynthesis in response to ambient or above-ambient ozone levels has been reported for a variety of tree species (Reich et al. 1987, Carlson 1979, Barnes 1972). Changes in carbon allocation to various carbohydrate fractions (Jensen 1981, Constanidou and Kozlowski 1979) or in the spatial patterns of allocation may also occur in response to ozone fumigation (Cooley and Manning 1987, McCool and Menge 1983). Impacts on either of these processes (photosynthesis or carbon allocation) could significantly affect rhizosphere processes and associations.

Probably the most ubiquitous and important of the rhizosphere associations is that formed between the host tree and mycorrhizal fungi. The key processes involved in this mutualistic association are translocation of photosynthate to the fungus (regulated to a greater or lesser extent by the fungus through establishment of a source-sink relationship) and enhanced uptake of key nutrients by the

fungus with subsequent release to the host plant. Disruption of the symbiosis, either through direct toxic effects on the mycosymbiont or through alterations in carbon supply, could have deleterious effects on the host.

Results of studies examining O_3 effects on mycorrhizae are conflicting. Reich and coworkers (1985) reported that mycorrhizal infection of northern red oak seedlings increased following ozone exposure, whereas no effect of O_3 on ectomycorrhizae of loblolly pine was detected by Mahoney et al. (1985). However, McCool and Menge (1983), working with endomycorrhizal tomatoes, observed reductions in infection of 46% after exposure to 150 ppb O_3 (3 hr, twice weekly). Even greater reductions were seen at 300 ppb, and dry weights of mycorrhizal plants were less than those of nonmycorrhizal plants similarly exposed. The authors proposed that O_3 changed the nature of the association from symbiotic to "pathogenic," due to competition for photosynthate between fungus and host.

Confusion is further increased when one considers possible interactive effects of ozone with acidic deposition (Shafer et al. 1985). In this case, mycorrhizae are subject not only to indirect effects through host responses, but are also vulnerable to changes in soil pH, soil nutrient status, and heavy metal solubilization.

A better understanding of ozone and acidic precipitation effects on whole plant carbon allocation and storage, with concurrent examination of effects on mycorrhizae, is needed. This paper presents results of an experiment designed to examine effects of ozone and acidic precipitation on carbon allocation and storage, and implications for mycorrhizal infection in loblolly pine seedlings. Starch was selected for study as it is the major reserve carbohydrate in woody plants. Given that roots often contain the highest concentrations of starch (Ebell 1969), starch concentrations in the roots were examined to assess the effects of ozone and acidic precipitation on carbon reserves. Cumulative effects on whole-plant carbon allocation patterns were examined using ^{14}C-labeling.

It was hypothesized that exposure to elevated O_3 would result in decreased carbon allocation to the roots of these seedlings, with resulting decreased starch content and mycorrhizal infection. Rain pH was hypothesized to interact with the O_3 treatment, possibly as an ameliorating factor, though all effects were expected to vary with family.

METHODS

This study utilized a subset of seedlings from an experiment examining the responses of 53 genotypes of loblolly pine to O_3 and acidic precipitation (McLaughlin et al. 1988). Seedlings from two of these families were selected for this study (designated families 8 and 9). These two families were among those included in an interlaboratory comparison of responses across participating laboratories within the Southern Commercial Forest Research Cooperative. All seedlings were grown in a 3:1 vermiculite:peat mixture, and inoculated with spore pellets of *Pisolithus tinctorius* (Pers.) Coker and Couch approximately 12 weeks prior to treatment.

Seedlings were exposed to three levels of ozone [charcoal-filtered air (CF or control), ambient air + 80 ppb O_3 (A80), and ambient + 160 ppb O_3 (A160)] and three levels of rain acidity (pH 5.2, 4.5, and 3.3) in an open-top field chamber factorial experiment for 12 weeks during the 1986 growing season (August 7 to

November 10). Ozone exposure statistics are given in Table 1. Complete details of the exposure systems and treatments are given in McLaughlin et al. (1988).

$^{14}CO_2$ Allocation

For the carbon allocation and starch analyses, 104 seedlings were selected (3 O_3 levels × 3 rain pHs × 2 families × 2 replications from 3 blocks). A 90 × 60 × 72 cm wood and clear Teflon chamber was used to expose the plants to ^{14}C-enriched CO_2 (360 ppm CO_2, 19.9 uCi L^1). High-intensity discharge sodium vapor lamps (400 W) provided illumination at light saturation conditions (500–600 uM m^2 s^1). The $^{14}CO_2$ gas was delivered into the chamber at a flow rate of 6 L min^1 (0.10 L s^1) for 30 sec. A small fan within the chamber ensured circulation of the gas. After the initial 30 seconds, ^{14}C injection was halted, and the air was circulated an additional 90 sec., then the chamber vented and the air pumped out of the chamber.

The plants were removed from the chamber, and a representative sample of secondary foliage was collected (approximately 0.02 g dry weight) from each seedling. This is referred to as the Day 0 (D_0) sample. The foliage sample was frozen immediately with liquid nitrogen, then stored frozen until dried to a constant weight in a forced-draft oven at 70°C. Subsamples of foliage were again collected 24 hr after tagging (Day 1) and after one week (Day 7). On Day 7, the seedlings were removed from the pots, separated into shoots and roots, assessed for mycorrhizal infection (see methods below) and frozen with liquid nitrogen. Prior to drying, these components were further separated into foliage, stem, and fine and coarse roots (<1.0 mm and ≥ 1.0 mm, respectively). Biomass of all samples and plant components was determined after drying. Fine roots, coarse roots and stems were ground to pass a 40-mesh Wiley mill screen. Samples were oxidized using a Packard Model 306 Tri-Carb sample oxidizer. Released CO_2 was trapped in scintillation cocktail and counted in a Packard Tri-Carb 460C automatic liquid scintillation counting system. Carbon allocation, expressed as the percent of the original (D_0) ^{14}C uptake of the individual seedling and as the percent of activity remaining in the plant after 7 days, was examined, and comparisons were made among plant components, across treatments and across families.

Starch Assays

Starch concentrations in the roots of the seedlings labeled with ^{14}C were assayed to determine sensitivity of carbon storage to ozone fumigation and rain chemistry.

TABLE 1.

Ozone exposure statistics for open-top chambers during the 1986 growing season (excerpted from McLaughlin et al. 1988).

	Treatments		
	CF	A80	A160
Mean O_3 concentration during exposure (ppb)	15	27	28
Total daytime dose (ppm × hr)	19.3	58.9	78.9
Daytime respite dose (ppm × hr)	12.6	22.4	23.4
Total dose (ppm × hr)	37.7	105	145

Starch concentrations were determined separately for the fine and coarse roots using an enzymatic hydrolysis method similar to that described by Haissig and Dickson (1979). Briefly, reducing sugars and pigments were extracted from 20 mg subsamples with a mixture of methanol:chloroform:water (12:5:3, v:v:v), and the residue dried overnight. After rewetting the sample with ethanol, 4 mL of distilled water were added, and samples were boiled for 10 min. to gelatinize starch. Starch was then hydrolyzed to glucose by a mixture of two enzymes, an alpha-amylase and an amyloglucosidase, during a 24-h incubation at 50°C. Glucose concentrations were measured colorimetrically by means of a glucose-oxidase peroxidase reagent (Sigma Chemical Company 1983).

Starch standards were prepared identically to tissue samples to determine that starch recovery was complete. Replicates of "standard" samples were run with each batch of tissue samples to assess variability of the method, and approximately 20% duplication of tissue samples was also used.

Mycorrhizal Responses

Seedlings were assayed for mycorrhizal colonization immediately prior to the initiation of exposure and after 6 or 12 weeks of exposure. At the 6-wk harvest, seedlings from all rain pH levels in the CF and A160 treatments were examined; in the A80, only the seedlings in the pH 4.5 rain treatment were assessed. Seedlings from all ozone × pH combinations were included in the final (12 wk) harvest.

Percent mycorrhizal colonization (PMC) was estimated by the visual assessment method (Grand and Harvey 1982). Whole root systems were examined individually, and the percent of short roots on each seedling that exhibited typical *P. tinctorius* morphology was estimated to the nearest 5%. Seedlings were blind-coded, to minimize bias. Root systems were assessed twice in random order, and the difference between first and second readings was calculated. If the difference exceeded 15%, the root system was assessed a third time. Percent mycorrhizal infection for each seedling was recorded as the mean of two or three readings. Mycorrhization was also quantified directly by microscopic determination of the proportion of mycorrhizal short roots to total short roots for a subsample of the root system. Standard errors of measurement were maintained at less than 5% of the mean.

Data Analysis

Carbon allocation and starch data were analyzed using analysis of variance techniques for a split-plot design, using SAS software (SAS Institute 1985) with family as the subplot. Individual and interactive effects of the independent variables block and family were tested. Mycorrhizal data were arcsine transformed prior to analysis of variance. Where mean comparisons were appropriate, they were conducted at the $P = 0.05$ level of significance unless otherwise indicated.

RESULTS

Biomass

Results of all analyses of variance are presented in Table 2. No statistically significant interactions of the main effects were detected for biomass, nor were

any significant effects of ozone concentration or rain pH detected for any of the biomass components. Total plant biomass was also unaffected. Statistically significant differences due to family were detected, however. Seedlings of family 8 were consistently the largest, both aboveground and belowground. Root:shoot ratios were lower in family 8, independent of treatment, indicating different carbon allocation patterns (Table 3).

^{14}C Allocation

During the first week after tagging, approximately 50 to 63% of the ^{14}C taken up by the seedlings was lost from the foliage, either through translocation elsewhere in the plant, or through respiration. Much of this reduction occurred within the first 24 hours after tagging. Total loss per plant 1 week after tagging [largely due to respiration (Ursino et al. 1968), with slight losses due to root exudation (Norby et al. 1987)] varied between the two families, averaging 10.7% for family 8 and

TABLE 2.

Results of statistical analyses for biomass, starch concentration and content, and carbon allocation. [ozone (OZ), rain pH (RAIN), family (FAM), NS = not statistically significant, * = statistically significant at $P = 0.10$ level of significance, ** = statistically significant at $P = 0.05$ level of significance.]

	Effect						
	OZ	RAIN	OZ*RAIN	FAM	FAM*OZ	FAM*RAIN	FAM*OZ *RAIN
Biomass							
Fine roots	NS	NS	NS	**	NS	NS	NS
Coarse roots	NS	NS	NS	**	NS	NS	NS
Foliage	NS	NS	NS	**	NS	NS	NS
Stem	NS	NS	NS	**	NS	NS	NS
Total biomass	NS	NS	NS	**	NS	NS	NS
Root:shoot	NS	NS	NS	**	NS	*	NS
Starch							
Fine roots (conc.)	NS	NS	NS	**	NS	NS	NS
Fine roots (cont.)	NS	NS	NS	**	NS	NS	NS
Coarse roots (conc.)	**	NS	NS	**	NS	NS	NS
Coarse roots (cont.)	NS	NS	NS	**	NS	NS	NS
Total roots (conc.)	*	NS	NS	**	NS	NS	NS
Total roots (cont.)	NS	NS	NS	**	NS	NS	NS
^{14}C Allocation							
Fine roots	NS	NS	NS	NS	NS	NS	NS
Coarse roots	NS	**	NS	**	NS	NS	NS
Total roots	NS	NS	NS	**	NS	NS	NS
Foliage	NS	NS	NS	**	NS	NS	NS
Stem	NS	NS	NS	NS	**	NS	NS
Loss	NS	NS	NS	**	NS	**	NS

TABLE 3.

Biomass components, carbon allocation, and starch concentration and content of loblolly pine seedlings by genotype after 12 weeks of treatment. Standard errors are given in parentheses.

Biomass

	Foliage	Stem	Aboveground biomass	Fine roots	Coarse roots	Total roots	Root: shoot
	(g)						
8	3.54A*	1.62A	5.15A	1.13A	0.95A	2.08A	0.397A
	(0.10)	(0.05)	(0.13)	(0.04)	(0.03)	(0.06)	(0.01)
9	2.23B	0.87B	3.07B	0.82B	0.49B	1.31B	0.426B
	(0.11)	(0.04)	(0.14)	(0.04)	(0.02)	(0.06)	(0.01)

^{14}C allocation

	Foliage	Stem	Fine roots	Coarse roots	Total roots	Loss from plant
	(%)					
8	50.5A	15.5A	17.6A	14.4A	32.0A	10.7A
	(2.8)	(1.1)	(1.1)	(0.8)	(2.2)	(1.0)
9	37.1B	15.1A	15.2A	10.5B	25.7B	27.7B
	(2.0)	(1.0)	(0.8)	(0.7)	(1.6)	(1.5)

Starch concentration and content

	Fine Roots		Coarse Roots		Total Roots	
	Concentration (mg g^1)	Content (mg)	Concentration (mg g^1)	Content (mg)	Concentration (mg g^1)	Content (mg)
8	29.58A	35.37A	36.85A	35.90A	32.83A	71.27A
	(1.8)	(3.2)	(2.2)	(2.8)	(1.5)	(4.5)
9	22.93B	20.00B	31.24B	16.13B	26.21B	36.13B
	(1.2)	(1.7)	(2.0)	(1.4)	(1.1)	(2.4)

* Means for a given treatment within the same column are not significantly different at the $P = 0.05$ level if followed by the same letter.

27.7% for family 9 (Table 3). This, along with greater total biomass of family 8 at harvest, suggests seedlings of this family are more efficient in utilizing carbon. Genetic differences in allocation of the labeled photosynthate to the different plant components at harvest were also evident, with family 8 allocating significantly more photosynthate to foliage and roots (coarse and total roots) than family 9. Although not statistically significant, a trend of increasing ^{14}C loss with ozone concentration was observed, with the loss of ^{14}C in the A160 treatment nearly double that observed for the CF treatment (Figure 1). The percent carbon allocated to coarse roots varied significantly with rain pH and was greatest in seedlings receiving the ambient (pH 4.5) rain treatment (Figure 2). No other statistically significant effects of rain pH on carbon allocation were detected (Table 2).

STARCH

Starch concentration and content of fine and coarse root starch content were found to vary between the two families (Table 3). Starch concentrations and

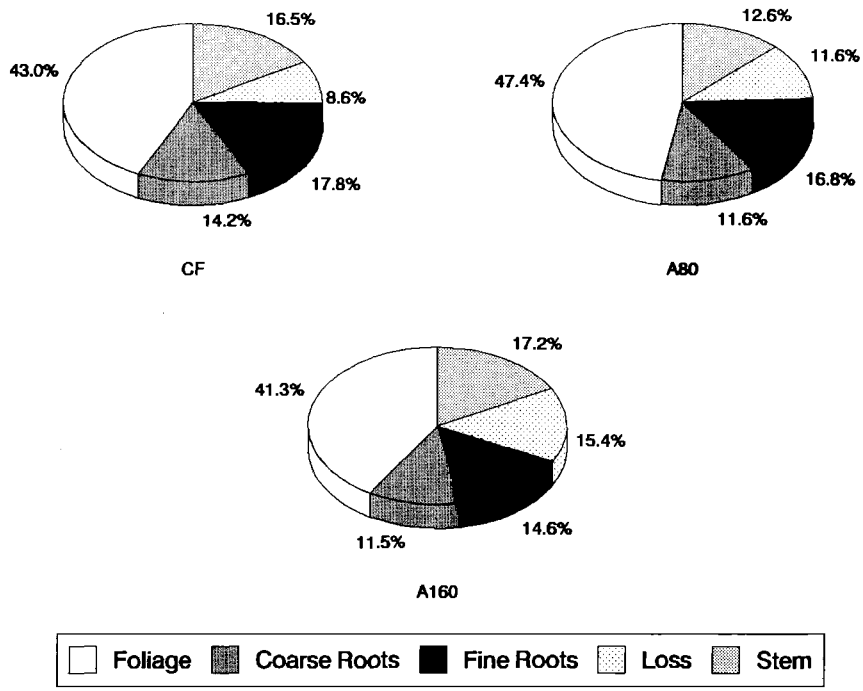

FIGURE 1. Whole-plant allocation of ^{14}C-photosynthate by loblolly pine seedlings as affected by ozone treatment.

content were greater in family 8. Total root system starch concentration also varied ($P = 0.10$) among ozone treatments (Figure 3). Concentrations were significantly greater in coarse roots of seedlings grown under the A80 treatment than in seedlings grown under either CF or A160 treatment. Mean fine root starch concentrations followed a similar response pattern, but the differences were not statistically significant. Rain pH did not affect root starch concentrations or content (Table 2).

MYCORRHIZAE

Percent colonization by *Pisolithus* was lower at the end of the 12 weeks' fumigation than was expected (Table 4). Given the extent of infection at the initiation of exposure, a mean infection rate of 70% or greater in the controls would not have been unexpected. Actual colonization ranged from 20 to 55% in the CF treatments. The PMC changed very little over the treatment period regardless of family or treatment.

No significant interactions of family, ozone, or rain pH were detected in the percentage of roots colonized for either harvest, nor was PMC affected by rain pH as a main effect (Table 4). The overriding main effect was family. Root infection by mycorrhizae was greater in family 8 at all harvests ($P = 0.0001$), despite no significant differences between the two families prior to exposure. Ozone effects were consistent across both families and were significant at 6 and 12 weeks at $P \leq 0.08$ and $P \leq 0.10$, respectively. The development of infection through time was different among O_3 treatments (Figure 4). For both families, infection in-

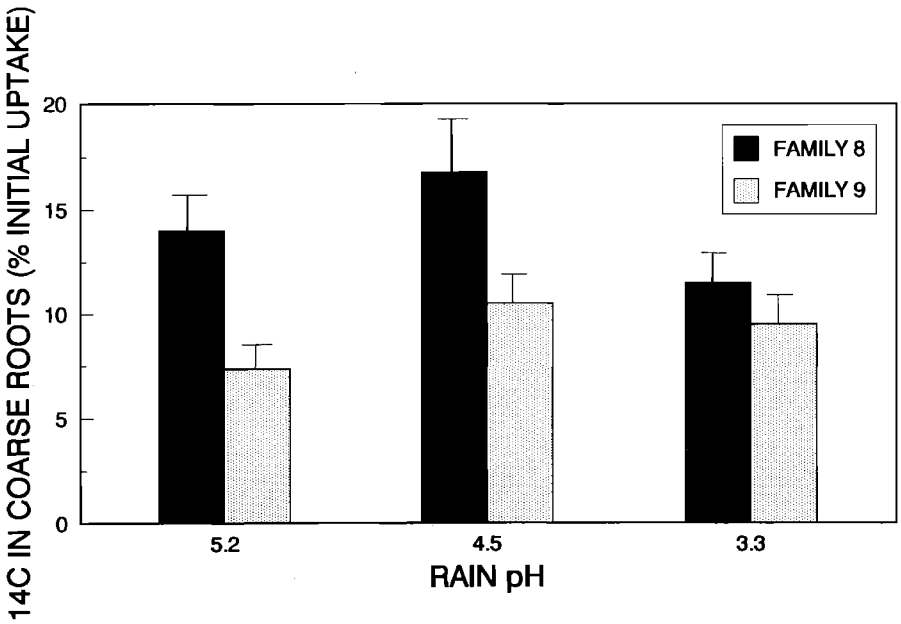

FIGURE 2. Allocation of ^{14}C to coarse roots of loblolly pine seedlings. Bars represent mean ± standard error of 16–18 seedlings.

creased for CF and A80 seedlings from 6–12 weeks. However, seedlings exposed to the A160 treatment were significantly less mycorrhizal than CF seedlings at 12 weeks, and equally or less mycorrhizal than the A160 seedlings from the 6-week harvest. Several seedlings in the A160 treatment, for family 9, had visibly abnormal mycorrhizae with reduced fine roots and dark-colored mycorrhizal tips, although no attempt was made in these assessments to differentiate between viable and nonviable mycorrhizae.

DISCUSSION

The most obvious differences in carbon allocation and PMC at harvest existed between the two families. Seedlings of family 8 consistently had the greater biomass, greater starch concentration and content, greater mycorrhizal infection, and lower root:shoot ratios. All of these suggest a more vigorously growing tree. No significant interactions of family, ozone, or rain pH were detected in the parameters under study. It is significant to note, however, that in the larger study, responses varied widely among the 53 families tested (McLaughlin et al. 1988). Generally, the two families described in this paper were less sensitive to elevated ozone levels than the average (McLaughlin et al. 1988).

Biomass data and carbon allocation patterns support the generally held presumption that a reduction in translocation to the belowground system will negatively affect mycorrhizal numbers and possibly mycorrhizal function. After 12 weeks, mycorrhizal infection in both families decreased with increasing ozone levels. In this study, however, there was no suggestion of a shift toward preferential allocation of photosynthate to mycorrhizal tissue at the expense of the host,

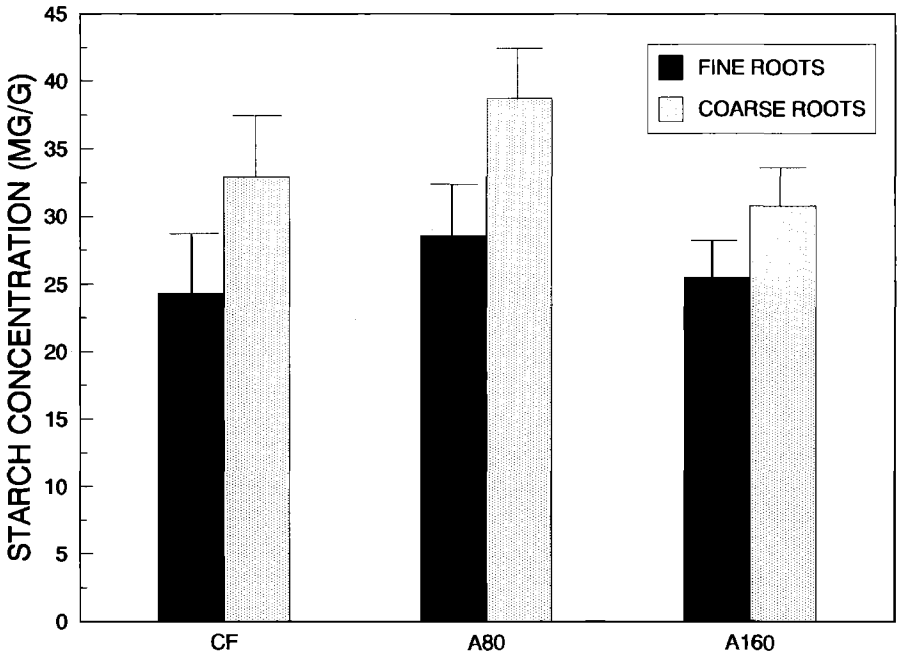

FIGURE 3. Root starch concentration as affected by ozone treatments, families 8 and 9 combined. Bars represent mean ± standard error of 34–36 seedlings.

as was reported by McCool and Menge (1983). In fact, relative reductions in PMC were greater than the reductions in fine root biomass, and starch storage in fine roots increased (Table 5), suggesting just the opposite. The greatest root starch concentrations were found in the coarse roots of seedlings receiving the A80

TABLE 4.

Percent mycorrhizal colonization of loblolly pine. Data represent the mean ± standard error.

		Ozone treatment		
Time	pH	CF	A80	A160
Family 8—40.6 % mycorrhizal short roots at time zero				
6 wk	3.3	32.8 ± 7		43.8 ± 5
	4.5	44.5 ± 9	32.9 ± 4	45.0 ± 4
	5.2	39.3 ± 4		40.4 ± 4
12 wk	3.3	54.8 ± 5	43.9 ± 4	45.2 ± 5
	4.5	54.0 ± 5	50.4 ± 4	44.7 ± 7
	5.2	44.6 ± 4	49.5 ± 6	34.0 ± 4
Family 9—32.6 % mycorrhizal short roots at time zero				
6 wk	3.3	20.8 ± 5		29.0 ± 7
	4.5	26.0 ± 4	29.0 ± 8	34.2 ± 6
	5.2	26.7 ± 4		34.0 ± 8
12 wk	3.3	35.0 ± 6	34.1 ± 9	25.8 ± 4
	4.5	36.8 ± 4	28.1 ± 5	37.8 ± 4
	5.2	36.6 ± 4	24.3 ± 5	26.4 ± 2

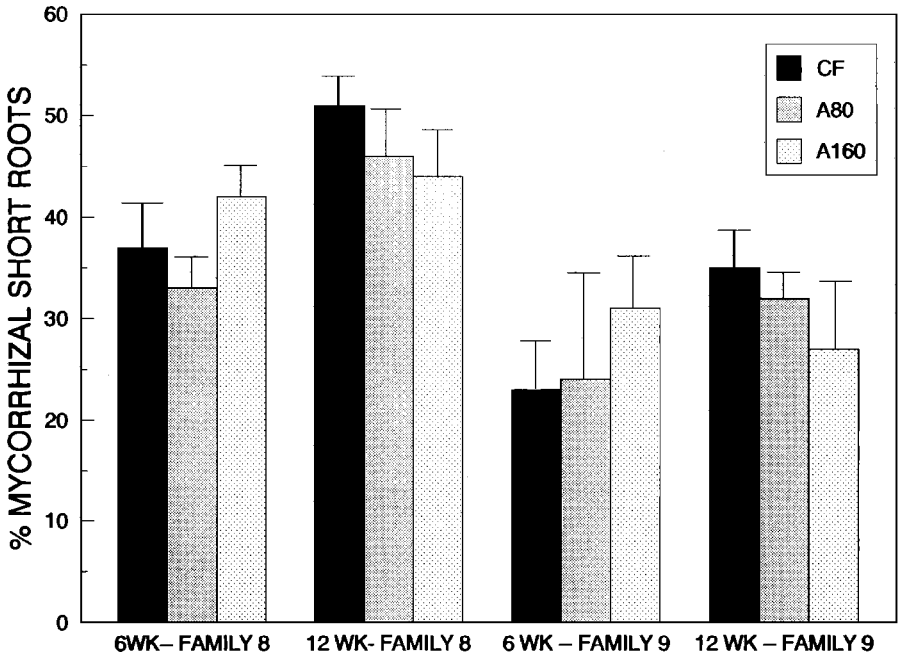

FIGURE 4. Percent mycorrhizal colonization of 2 families of loblolly pine after 6 or 12 weeks' exposure to ozone, pooled across pH levels. Bars represent mean ± standard error of 23–28 seedlings.

treatment, while starch concentrations in roots of A160 seedlings were not significantly different from those in roots of CF plants (Figure 3).

Slankis (1973) presented evidence from several sources that mycorrhizal auxins enhance hydrolysis of starch to soluble sugars. Thus, a reduction in mycorrhizal infection should be reflected in higher fine root starch concentrations. This pattern was observed in this study; however, the relationship between PMC and root starch was not statistically significant. Thus it may be inferred that the increased sink strength was due to increased root growth at the intermediate ozone level.

TABLE 5.

Comparative response of ^{14}C photosynthate allocation to roots, root biomass, starch concentration, percent mycorrhizal infection, photosynthesis and estimated respiratory losses of loblolly pine seedlings exposed to ozone for 12 weeks.

	Response[a]	
	A80	A160
Allocation of ^{14}C to fine roots	−6	−18
Allocation of biomass (fine roots)	+9	−3
Starch concentration (fine roots)	+20	+8
% Mycorrhizal infection	−9	−18
Photosynthesis[b]		−39
Respiratory losses	+35	+79

[a] Responses are expressed as a % of CF values.
[b] Data from Hanson et al. 1989.

A stimulatory effect on growth at low ozone concentrations has been documented for a number of loblolly pine families (McLaughlin et al. 1988), but the mechanism as yet is unknown.

Acid deposition within the range examined had no effect on quantifiable mycorrhizal infection, as predicted by Visser and coworkers (1987). However, no measure of mycorrhizal "effectiveness" was employed. Mycorrhizal benefits to host species are not always simply correlated with numbers of infected short roots, so failure to find changes in PMC due to acid deposition does not rule out the possibility of a change in mycorrhizal effectiveness. Ozone, also, could affect the symbiosis in ways that are not related to PMC. Further study should examine some aspect of mycorrhizal function under both elevated ozone levels and acidic deposition, to define the physiological role of mycorrhizae in tree response to pollutants.

McLaughlin and coworkers (1982) hypothesized that a decline of ozone-sensitive field-grown white pine was due to increased respiratory activity and altered carbon allocation patterns. Changes in patterns of respiration and carbon allocation at harvest with increasing ozone were observed in this study, along with decreases in mycorrhizal infection. Diminished photosynthesis of these seedlings was also recorded (Hanson et al. 1989). If such patterns were continued over a long period of time, a decline similar to that observed for white pine might be predicted for these loblolly pine. The measured growth slowdown of southern pines reported by Sheffield and Cost (1987), while not directly attributable to increased air pollution, lends further importance to this hypothesis. However, further research examining the long-term effects of ozone and acidic deposition on the physiology of loblolly pine is needed before such predictions can be made.

LITERATURE CITED

BARNES, R.L. 1972. Effects of chronic exposure to ozone on soluble sugar and ascorbic acid contents of pine seedlings. Can. J. Bot. 50:215–219.

BLUM, U., and D.T. TINGEY. 1977. A study of the potential ways in which ozone could reduce root growth and nodulation of soybean. Atmos. Env. 11:737–739.

CARLSON, R.W. 1979. Reduction in the photosynthetic rate of *Acer, Quercus,* and *Fraxinus* species caused by sulfur dioxide and ozone. Environ. Poll. 18:159–170.

CONSTANTINIDOU, H.A., and T.T. KOZLOWSKI. 1979. Effects of sulfur dioxide and ozone on *Ulmus americana* seedlings. II. Carbohydrates, proteins, lipids. Can. J. Bot. 57:176–184.

COOLEY, D.R., and W.J. MANNING. 1987. The impact of ozone on assimilate partitioning in plants: A review. Environ. Pollut. 47(2):95–113.

EBELL, L.F. 1969. Specific total starch determinations in conifer tissue with glucose oxidase. Phytochem. 8:25–26.

GRAND, L.F., and A.E. HARVEY. 1982. Quantitative measurement of ectomycorrhizae in plant roots. P. 157–164 *in* Methods and principles of mycorrhizal research, Schenck, N.C. (ed.). Am. Path. Soc., St. Paul, MN.

HAISSIG, B.E., and R.E. DICKSON. 1979. Starch measurement in plant tissue using enzymatic hydrolysis. Physiol. Plant 47:151–157.

HANSON, P.J., S.B. MCLAUGHLIN, and N.T. EDWARDS. 1989. Net CO_2 exchange of *Pinus taeda* shoots to variable ozone levels and rain chemistries in field and laboratory settings. Physiol. Plant. (In press.)

JENSEN, K.F. 1981. Air pollutants affect the relative growth rate of hardwood seedlings. USDA Forest Service Research Paper NE-470, Northeastern Forest Experiment Station, Broomall, PA.

McCool, P.M., and J.A. Menge. 1983. Influence of mycorrhizae on the growth of loblolly pine seedlings exposed to ozone and sulfur dioxide. Phytopath. 75:679–682.

McLaughlin, S.B. 1985. Effects of air pollution on forests: A review. J. Air Poll. Control Assoc. 29:157–161.

McLaughlin, S.B., et al. 1988. Comparative sensitivity, mechanisms, and whole-plant physiological implications of response of loblolly pine genotypes to ozone and acid deposition. Oak Ridge Nat. Lab. Tech. Rep. ORNL/TM-10777. Oak Ridge, TN.

McLaughlin, S.B., et al. Growth response of 53 open-pollinated loblolly pine (*Pinus taeda* L.) families to ozone and acidic rain. For. Sci. (In review.)

McLaughlin, S.B., et al. 1982. Effects of chronic air pollution stress on photosynthesis, carbon allocation and growth of white pine trees. For. Sci. 28(1):60–70.

Reich, P.B., et al. 1987. Effects of ozone and acid rain on white pine (*Pinus strobus*) seedlings grown in five soils. I. Net photosynthesis and growth. Can. J. Bot. 65(5):977–987.

Reich, P.B., and R.G. Amundson. 1985. Ambient levels of ozone reduce net photosynthesis in tree and crop species. Science 230:566–570.

SAS Institute, Inc. 1985. SAS user's guide: Statistics, version 5 edition. SAS Institute, Cary, NC.

Shafer, S.R., et al. 1985. Formation of ectomycorrhizae on *Pinus taeda* seedlings exposed to simulated acidic rain. Can. J. For. Res. 15:66–71.

Sigma Chemical Company. 1983. The enzymatic determination of glucose. Sigma Tech. Bull. No. 510. Sigma Chemical Co., St. Louis, MO.

Slankis, V. 1973. Hormonal relationships in mycorrhizal development. P. 231–298 *in* Ectomycorrhizae: Their ecology and physiology, Marks, G.C., and T.T. Kozlowski (eds.). Academic Press, New York.

Visser, S., R.M. Danielson, and J.F. Parr. 1987. Effects of acid-forming emissions on soil microorganisms and microbially-mediated processes. *In* Preparations for the Acid Deposition Research Program. Kananaski Centre for Environ. Res., University of Calgary and U.S. Dept. Agric., Beltsville, MD. ARDP-B-02-07.

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