

THREE-YEAR GROWTH RESPONSES OF *PINUS TAEDA* L. TO SIMULATED RAIN CHEMISTRY, SOIL MAGNESIUM STATUS, AND OZONE¹

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(Received February 11, 1991; revised April 18, 1991)

Abstract. Height, diameter, and biomass were measured for loblolly pine (*Pinus taeda* L.) seedlings grown in soil containing 15 or 35 $\mu\text{g Mg g}^{-1}$ and exposed from May to October in 1987, 1988, and 1989 to three O_3 concentrations (sub-ambient, ambient, or twice-ambient) and to rain pH levels of 3.8 or 5.2. Reduction in biomass accumulation in seedlings exposed to twice-ambient O_3 vs sub-ambient O_3 was 14% ($P = 0.03$) in 1987, 11.4% ($P = 0.002$) by 1988, and 8% ($P = 0.15$) by 1989. The greatest height growth occurred in seedlings exposed to twice-ambient O_3 , and the greatest stem diameter growth occurred in seedlings exposed to sub-ambient O_3 . A comparison of stem volume (d^2h) with stem biomass suggested that tissue density was reduced by elevated O_3 . Biomass accumulation response to rainfall chemistry was small (5.5% reduction in the low pH treatment in 1989) and not statistically significant for most plant tissues. Growth response to soil Mg status was not significant. However, in 1989 treatment interactions between rainfall chemistry and soil Mg status were observed. Height was 5% greater ($P = 0.02$) and biomass was 6% greater ($P = 0.10$) in seedlings grown in higher-Mg soil and receiving higher-pH rainfall than seedlings grown in any of the other pH-Mg treatment combinations. The data suggest direct adverse effects of near ambient O_3 and indirect, slower acting and interacting adverse effects of rainfall chemistry and soil nutrient status on growth of loblolly pine.

1. Introduction

Unexplained reductions in net annual growth of yellow pines in southeastern North America have been reported (Sheffield *et al.*, 1985), and wet and dry deposited air pollutants were proposed as potential stresses. Ozone injury to pine species in California has been documented (Miller *et al.*, 1963; McBride *et al.*, 1975). However, evidence confirming or refuting a linkage between growth decline of forest trees and air pollution is fragmentary (Lucier and Stout, 1988).

A number of hypotheses have been offered to explain the growth decline of forest trees (McLaughlin, 1985). One hypothesis is that direct phytotoxic effects of O_3 may result in leaf tissue damage and reduced net photosynthesis. Tissue damage in the leaves may lead to indirect effects on growth and physiology. For example, increased C utilization for repair of O_3 -damaged leaf tissue may result in decreased C availability for growth. Another hypothesis is that the effects of S and N deposition and associated H^+ on foliar leaching and soil nutrient status

may interact with O₃ to reduce growth. Foliar mineral deficiencies in general and Mg deficiency specifically can be attributed to (1) O₃-induced reductions in mineral uptake from the soil because of reduced plant vigor or root surface area or both, (2) reduced availability of nutrients in the soil because of accelerated cation leaching, and (3) increased foliar leaching as a result of wet and dry pollutant deposition (Prinz *et al.*, 1982). This paper presents results of a 3-yr study designed to examine the hypothesis that O₃, acidic rainfall, and soil Mg deficiency interact to influence the growth of loblolly pine (*Pinus taeda* L.).

2. Materials and Methods

RESEARCH FACILITY

The study was conducted at an open-top chamber facility located at the Oak Ridge National Environmental Research Park near Oak Ridge, Tennessee. The facility, modified slightly from that described by Johnston *et al.* (1986), consisted of 36 open-top chambers equipped with a rainfall exclusion/addition system and an O₃ addition/monitoring system.

SOIL AND SEEDLING PREPARATION

Soil was collected from the A horizon of a fine loamy silicious, mesic Typic Hapludult (Lilly Series). The soil was collected from a former hardwood forest site that had been prepared for conversion to pine. Soil was sieved and mixed (80:20, v:v) with sand derived from the sandstone residuum in which the soil had formed. The addition of sand changed the texture classification of the soil from loam to sandy loam.

The sieved and mixed soil was placed in 24-L plastic pots (18-kg oven-dry equivalent per pot), and fertilizer (0.7 g N, 1 g P, 0.5 g K, 10.9 g Ca, 0.02 g Zn, and 0.02 g Cu) was added to each pot and thoroughly mixed with the soil. Nutrient additions were intended to provide adequate levels of major and minor nutrients, with the exception of Mg (South and Davey 1983). The level of extractable Mg (double acid extracted and analyzed by inductively coupled plasma-atomic emission spectroscopy) was unaltered (15 µg g⁻¹) in one-half of the pots (to produce a near-deficient condition), whereas the remainder of the pots received a MgSO₄ supplement to achieve 35 µg g⁻¹ of Mg. Additional N as NH₄NO₃ (1 g pot⁻¹, 15 g m⁻²) was supplied in solution at monthly intervals during each growing season in an attempt to increase plant demand for Mg and thus enhance the possibility of a Mg deficiency response.

In mid-April of 1987, a total of 1296 bare-root 1-yr old seedlings of similar height and diameter were transplanted into the pots (1 seedlings per pot, 36 pots per chamber). Seedlings were provided by the Weyerhaeuser Company nursery at New Bern, North Carolina, and were from seed of Weyerhaeuser family number 8-127 (Adams *et al.*, 1988).

PRECIPITATION AND OZONE TREATMENTS

Simulated rain was added to each chamber throughout the entire study (including winter) in an amount based on the measured volume of each natural precipitation event and was added immediately after a rainfall during cloud cover or very early in the morning. This schedule was periodically modified to permit watering during extended periods of dry weather to reduce seedling water stress. Simulated rain was prepared by adding a chemical stock solution to deionized water to create ionic proportions equivalent to those of natural rainfall (Irving, 1985), with the exception that no Mg was added. Appropriate amounts of H_2SO_4 and HNO_3 (7:3 equivalent basis) were added to provide two pH levels (3.8 and 5.2). The opening above each chamber was shielded during rainfall events and at night. A 30 cm space between the rain shields and the tops of the chambers permitted continuous circulation of air through the chambers.

Three O_3 treatment levels were used in the study. Twelve of the chambers received sub-ambient levels through the use of charcoal filters which removed about half of the O_3 in ambient air, twelve received ambient concentrations, and twelve received twice-ambient concentrations. Air was injected into each chamber at a flow rate of about $70 \text{ m}^3 \text{ min}^{-1}$ through a plenum located in the lower half of the chamber. Ozone was generated from dried ambient air with an electrical discharge ozone generator equipped with an internal compressor and drying system (Ozone Research and Equipment Corporation Model 03-Sp33-Ar Ozone Generator). Twenty-four hr per day O_3 treatments were continued from late April through September of each yr. Ozone delivery rate was regulated continuously (both day and night) by a computer-based monitoring and control system operating in a feedback control loop to provide twice the ambient concentrations (McEvers *et al.*, 1989).

Ozone concentrations in each chamber were measured at 20-min intervals for 110 s with a monitoring system that included three Dasibi Model 1003PC fluorescent O_3 monitors. Seasonal patterns of O_3 concentrations are presented in Figure 1. The relatively low levels of O_3 in the 'twice-ambient' treatment in July 1988 was due to a 10 d breakdown of the O_3 generator. The breakdown plus lower production efficiency of the O_3 generator in 1988 and 1989 resulted in an average 'twice-ambient' exposure level of $1.5 \times$ ambient in 1988 and $1.7 \times$ ambient in 1989. The diurnal characteristics of ambient O_3 at this site are similar to those in low-elevation sites in eastern North America (Meagher *et al.*, 1987). Even though O_3 was generated 24 hr d^{-1} the concentrations at night in the twice ambient chambers seldom exceeded 30 nL L^{-1} because of very low nighttime ambient concentrations at the study site (Edwards *et al.*, 1990). Likewise during rainfall events ambient O_3 concentrations typically decreased to 10 to 20 nL L^{-1} .

Ozone generation from ambient air resulted in N deposition to the foliage of seedlings receiving twice ambient O_3 in amounts equivalent to about 6% of the plants total annual N demands vs about 1% in seedlings grown in ambient air, but about 80% of the N surface deposited as HNO_3 was washed off in throughfall

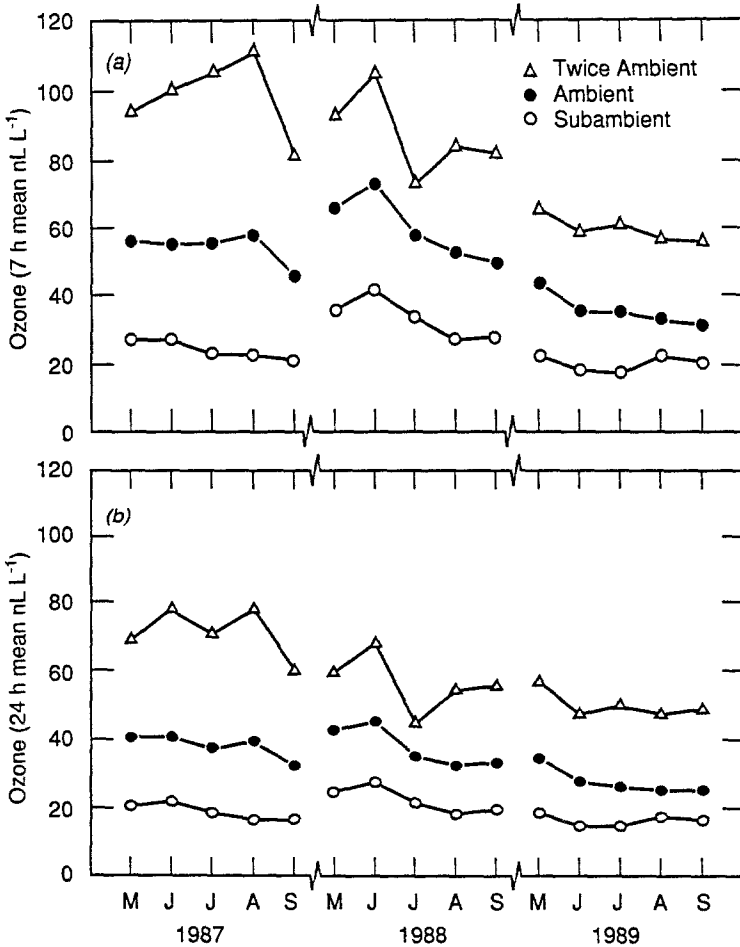


Fig. 1. (a) Monthly mean 7 hr (1000–1700 hr) O₃ concentrations and (b) monthly mean 24 hr O₃ concentrations in the three treatments maintained in the open-top chambers.

(unpublished data). Given these results we concluded that HNO₃ formation by the O₃ generator was physiologically insignificant relative to other modes of N acquisition by the seedlings.

GROWTH MEASUREMENTS

Seedlings designated for harvest at the end of the third growing season were used for periodic height and diameter measurements. Seedlings were measured in May and thereafter at 2-mo intervals. Two measurements of stem diameter were taken with electronic digital calipers (sensitivity = 0.01 mm) at right angles at 5 cm above the soil surface and then averaged. Height was measured as the distance between the soil surface and the base of the apical bud. At the end of the third yr relative stem densities were calculated by dividing stem dry weight by d²h (diameter squared × height) of each seedling.

In October of each yr one-third (432) of the seedlings (12 per chamber; six per Mg treatment) were removed from the chambers, harvested, and separated into fine roots (<1 mm), coarse lateral roots (>1 mm), stems + branches, and current- and previous-yr foliar flushes. Current yr flushes (generally 3 flushes per yr) were also separated. Biomass was determined for each component after the tissues had been dried to a constant weight at 70 °C.

EXPERIMENTAL DESIGN AND STATISTICAL ANALYSIS

A split-plot, randomized complete block design was used with O₃ and rainfall pH as main plots and soil Mg status as split-plots within each chamber. Pots were rearranged within the chambers at 2-mo intervals to minimize positional effects. Each treatment combination was replicated six times, with six seedlings per replication. Repeated measures of height and diameter were evaluated by analysis of covariance with initial height or diameter as a co-variate. Analysis of variance techniques were used to evaluate the biomass data. When a significant ($P \leq 0.10$) O₃ response was found with the analysis of variance model, adjusted (least squares) biomass means were compared to determine which of the means differed significantly.

3. Results and Discussion

TREATMENT INTERACTIONS

There were no treatment interactions between O₃ and rainfall chemistry or soil Mg status. The only interactions observed were between soil Mg status and rainfall chemistry in 1989. Heights of seedlings grown in higher Mg soil and receiving higher pH rainfall were 5% greater in 1989 ($P = 0.02$) than seedlings grown in any of the other pH-Mg treatment combinations. Similarly, biomass of seedlings grown in the higher Mg soil, higher pH treatment combination was greater by 6% ($P = 0.10$) in 1989 than in any of the other pH-Mg treatment combinations. The biomass differences were fairly uniform across all tissue types with the greatest difference in the fine roots (8%, $P = 0.05$). If the lower-pH rainfall treatment caused increased Mg leaching rates from the soil or from the plant tissues we should expect to see lower Mg concentrations in the plant tissues. However, no decrease in Mg concentrations was found in response to the lower-pH treatment in any of the plant tissues sampled at the end of the 1988 growing season (Edwards *et al.*, 1991) or in 1989 (unpublished data). The lack of foliar leaching in response to rainfall chemistry could be because the rainfall pH treatments represented chronic levels of acidity, and consequently were not acidic enough to elicit foliar leaching responses. All of the tissues from seedlings grown in the lower-Mg soil did have significantly ($P \leq 0.01$) lower Mg concentrations than those from seedlings grown in the higher-Mg soil.

WHOLE-PLANT RESPONSES TO OZONE

A trend of reduced total plant biomass accumulation in loblolly pine seedlings with increasing exposure levels of O₃ was observed during each of the 3 yr of this study (Table I and Figure 2a) and whole-plant biomass differences between twice-ambient and subambient O₃ treated seedlings were statistically significant ($P \leq 0.10$) at the end of 1987 and 1988 but not by the end of 1989 ($P = 0.15$). The growth reductions may have been caused by O₃-induced decreases in net photosynthesis (Reich and Amundson, 1985; Norby *et al.*, 1985; Hanson *et al.*, 1988), although unpublished data (G.E. Taylor, Jr. and C. A. Gunderson) show no O₃ associated changes in net photosynthesis of loblolly pine per unit leaf area. Growth

TABLE I

Summary of *Pinus taeda* L. seedling growth response to O₃, rain pH, and soil Mg levels during 3 yr of treatment

Treatment	Average Total Biomass Plant ^a						
	O ₃	pH	Mg	1987	1988	1989	n
				(g dry wts)			
Subambient	3.8	1		48.9(1.6)ab	150.9(4.8)a	299.8(9.7)a	36
Ambient				43.5(1.6)b	142.3(4.7)a	292.4(9.5)a	
Twice-ambient				44.7(1.6)b	149.7(5.4)a	306.3(13.5)a	
Subambient	3.8	2		53.1(1.8)a	146.9(4.9)a	322.2(13.2)a	36
Ambient				44.1(1.8)b	141.5(4.3)a	290.3(9.8)b	
Twice-ambient				45.1(1.7)b	145.4(5.2)a	302.9(12.4)b	
Subambient	5.2	2		53.1(2.2)a	158.3(2.8)a	345.0(10.3)a	36
Ambient				48.3(1.7)a	160.7(5.3)a	337.0(13.1)a	
Twice-ambient				41.5(1.7)b	126.6(3.4)b	292.5(10.1)b	
Subambient	5.2	2		52.8(2.1)a	168.0(4.8)a	331.0(10.6)a	36
Ambient				48.2(1.8)b	156.2(5.8)a	322.8(14.3)a	
Twice-ambient				45.0(1.5)b	132.2(3.5)b	291.0(8.4)b	
Subambient	- ^c	-		51.2(0.9)a	156.1(2.3)a	324.5(5.6)a	144
Ambient	-	-		46.0(0.9)b	150.0(2.6)b	310.0(6.1)a	
Twice-ambient	-	-		44.1(0.8)b	138.0(2.3)c	298.0(5.7)a	
-	3.8	-		46.6(0.7)a	146.1(2.0)a	302.1(4.7)a	216
-	5.2	-		47.7(0.8)a	150.2(2.1)a	319.8(4.8)a	
-	-	1		46.2(0.7)a	147.9(2.0)a	312.2(4.7)a	216
-	-	2		48.1(0.8)a	148.3(2.1)a	309.6(4.9)a	

^a 1 = 35 µg Mg g⁻¹; 2 = 15 µg Mg g⁻¹.

^b Means followed by the same letter are not significantly different ($P \leq 0.1$); standard errors of the mean are indicated parenthecally.

^c Treatment regimes indicated by a dash represent values averaged across treatments.

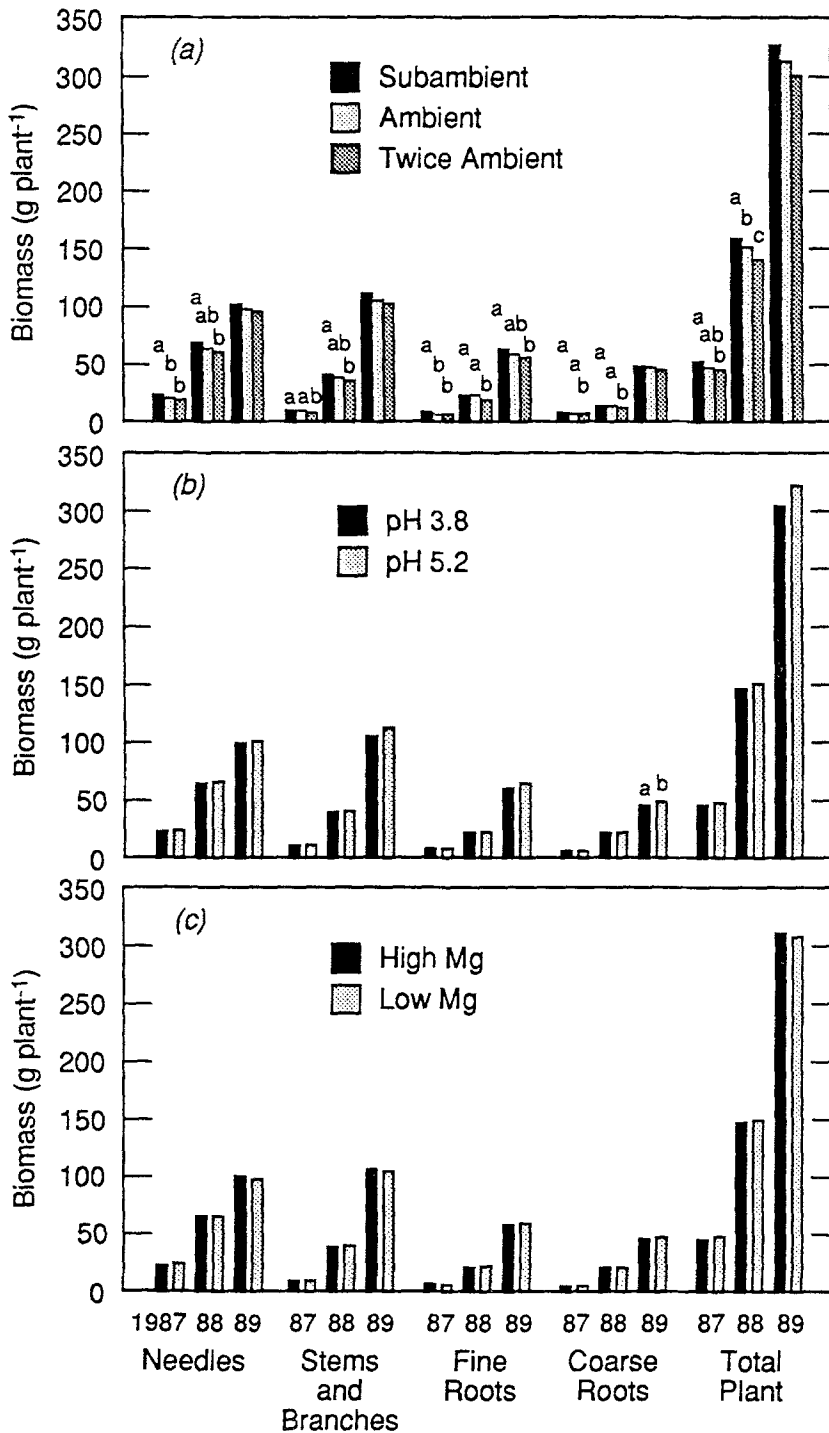


Fig. 2. Whole-plant and individual tissue biomass responses of loblolly seedlings to (a) O₃ concentrations, (b) rainfall pH, and (c) soil Mg status during each yr of a three yr treatment regime. The values are means (n = 144 for O₃; n = 216 for pH and soil Mg). Means with the same letter and bars without letters are not significantly different (P ≤ 0.1).

reduction may also have been caused by increased dark respiration (Skarby *et al.*, 1987) or by increased whole plant respiration (Adams *et al.*, 1990).

The reduced biomass accumulation in response to O₃ occurred without visible needle damage at any time during the 3-yr study. Also, Edwards *et al.* (1990) reported no reduction in needle pigments in response to O₃ during the first yr of this study. Pigment analyses continued through the second yr and no adverse O₃ effects on needle pigment concentrations were detected. The lack of visible needle injury was surprising because in a previous study at an adjacent site with the same loblolly family, Adams, *et al.* (1988) observed visible O₃ damage to needles. However, the seedlings used in the previous study were started from seeds only 3 mo prior to elevated O₃ exposure and therefore their needles may have been more delicate and susceptible to O₃ damage than the needles of the 1-yr old seedlings used in this study. Also, in the previous study O₃ was added in a constant addition mode (ambient + 60 nL L⁻¹) rather than the proportional addition mode used in this study.

The whole-plant growth responses observed in this study support results from shorter term open-top and growth chamber studies (Kress and Skelly, 1982; Chevone *et al.*, 1984; Shafer *et al.*, 1987; Adams *et al.*, 1988; Shafer and Heagle, 1989; McLaughlin *et al.*, 1989), that demonstrated adverse effects of elevated O₃ concentrations on the growth of loblolly pine seedlings.

The percentage reduction in whole-plant biomass accumulation in response to the O₃ treatment declined during the last 2 yr of the 3-yr exposure (Figure 3). Percentage reduction in biomass accumulation by ambient vs sub-ambient O₃ declined

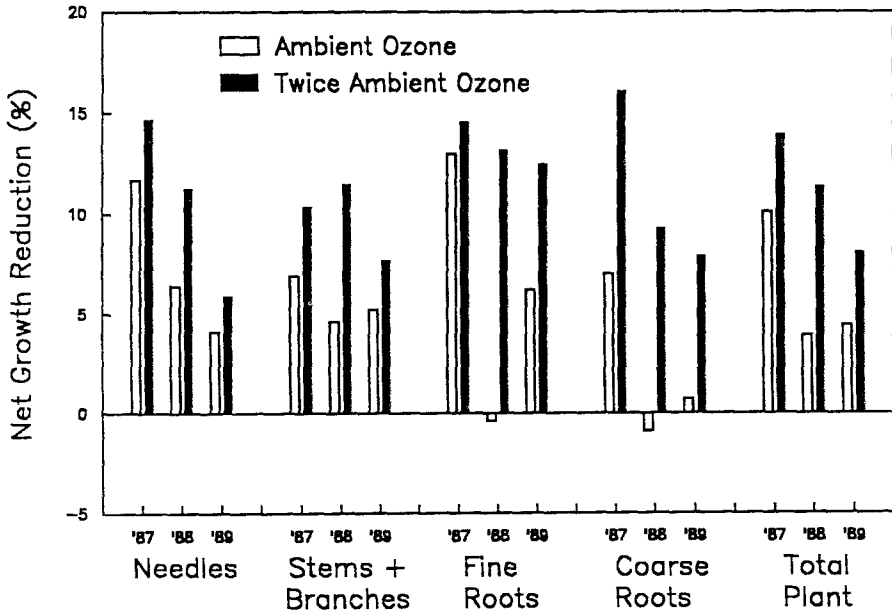


Fig. 3. The percentage reduction in biomass accumulation of loblolly seedling tissues by ambient and twice-ambient levels of O₃ (compared to subambient levels) each yr of the three-yr treatment period.

to 4% in 1988 and 4.4% in 1989 following an initial 10% reduction in biomass accumulation in 1987. Reduction in biomass accumulation in seedlings exposed to twice-ambient O_3 vs sub-ambient O_3 was 14% in 1987, 11.4% in 1988, and 8% in 1989. The decline in percentage growth reduction by twice-ambient O_3 most likely resulted from reduced exposure levels of O_3 during each succeeding yr of the study (Figure 4). The decline in exposure levels was caused by reduced ambient O_3 levels in 1989 and to the reduced efficiency of our O_3 generator in 1988 and 1989. Another possible cause of the apparent reduced damage to the seedlings in 1989 may be related to increased moisture stress to the seedlings in 1989. Average monthly simulated rainfall for the 1987 and 1988 growing seasons (April through September) and for the first half of the 1989 growing season was only 8 cm as compared to the 25 yr monthly average natural rainfall of 10.5 cm for the same months (Local Climatological Data, 1972). Simulated rainfall during July through September of 1989 was 30% above the 25 yr natural rainfall average and is reflected in the greater height and diameter growth of the seedlings in the last half of the 1989 than for the same months of the 1987 and 1988 growing seasons (Figure 5). Even though the amount of water delivered to the seedlings during the 1987 and 1988 growing seasons and the first half of the 1989 growing season was below the 25 yr average rainfall amounts, the seedlings were probably more water stressed the last 2 yr, especially during the first half of the 1989 growing season, than during 1987 because of increased water demands as the seedlings increased in size. This may have been exacerbated by root crowding in the pots during the third yr. In fact the water stress in the early part of the 1989 growing season may have resulted in an observed increase in the root/needle biomass ratio by the end of 1989. Root

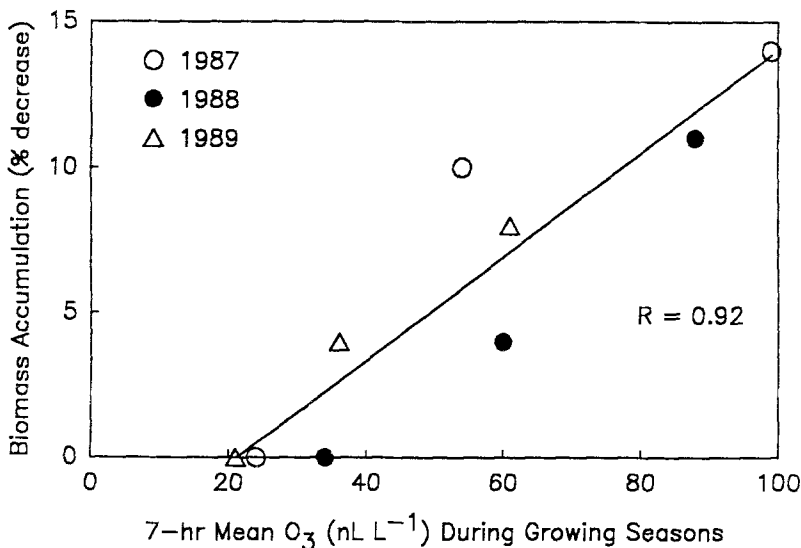


Fig. 4. Whole-plant biomass response (% decrease using subambient as baseline) of loblolly seedlings to increasing concentrations of O_3 following each yr of a three yr treatment regime.

biomass (averaged across all treatments) increased by 68% between 1987 and 1988 and by 59% between 1988 and 1989, whereas needle biomass increased by 66% between 1987 and 1988 but only by 34% between 1988 and 1989. Thus root/needle ratios increased substantially in 1989 from an average of 0.69 and 0.68 in 1987 and 1988, respectively, to 1.12 in 1989. This apparent increased water stress to the seedlings during the first half of 1989 may have resulted in reduced O₃ damage because stomatal closure in response to the water stress which could have decreased the amount of O₃ entering the needle tissues through the stomatal openings. Such a response has been observed in loblolly pine (Taylor *et al.*, 1989) and in soybean [*Glycine max* Merr] (Amundson *et al.*, 1986).

A number of studies have reported adverse effects of O₃ on height and diameter growth of loblolly pine (Kress *et al.*, 1988; Shafer *et al.*, 1987; Shafer and Heagle, 1989; Adams *et al.*, 1988). However, height and diameter responses to O₃ exposures

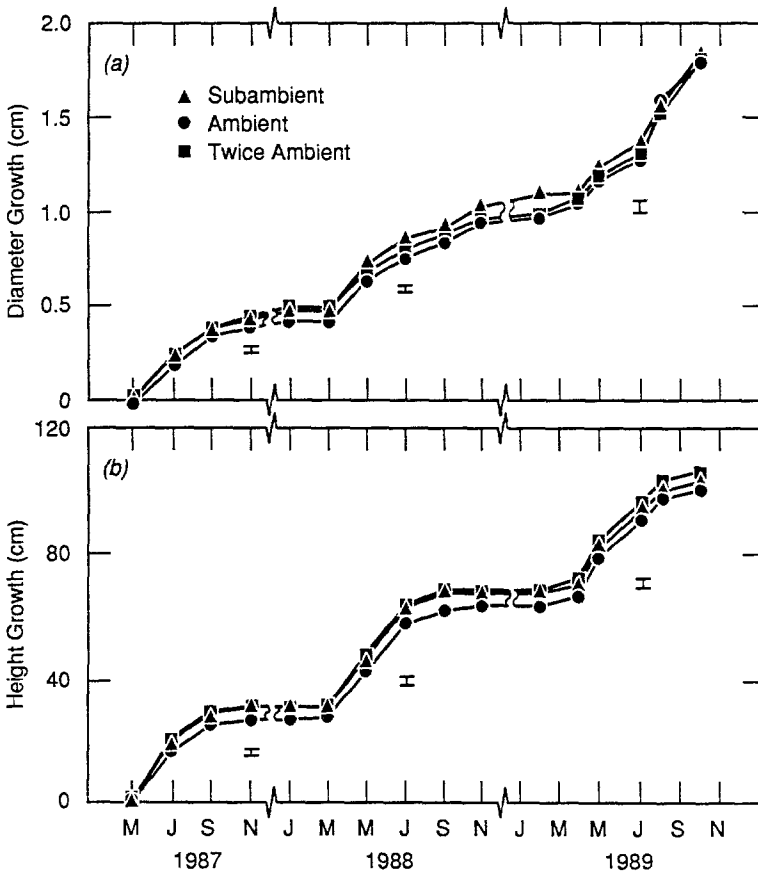


Fig. 5. Mean monthly (a) height and (b) diameter growth in *Pinus taeda* L. seedlings as a function of O₃ treatments between May 1987 and November 1990. Values are mean differences between measurements at planting and the date indicated. Bars are 1 standard error averages for each growing season (n = 144).

did not accurately reflect the seedling biomass accumulation responses found in this study. At the end of the 1987 and the 1988 growing seasons seedlings receiving twice-ambient O₃ treatments were equal in stem diameter and greater in height ($P = 0.043$ in 1987 and 0.035 in 1988) than those grown in ambient air (Figure 5), yet had less biomass in all plant organs that were measured (Figure 2a). In the first yr results of this study (Edwards *et al.*, 1990), this phenomenon was explained by O₃ effects on tissue density or on biomass partitioning between stems and branches (i.e. reduced branch biomass accumulation in the twice-ambient treated seedlings). This could not be evaluated with the first-yr data because the stems and branches were not separated before being weighed. However, the third yr stems and branches were separated and the results demonstrated a 5.5% decrease ($P \leq 0.1$) in relative stem density in seedlings exposed to twice-ambient O₃ as compared to ambient O₃.

The reduced tissue density associated with elevated O₃ could have resulted from early dormancy induction by O₃, as observed in loblolly seedlings by Adams *et al.* (1988), because earlier onset of dormancy and cessation of cambial activity could increase the proportion of low-density spring wood to high-density summer wood. To our knowledge there have been no other reports of decreased stem density in response to O₃, but if correct such a phenomenon would have important implications for commercial wood producers. Wood specific gravity (directly correlated with wood density) has traditionally been the most important single characteristic in the program of genetic manipulation of forest trees on a large scale, especially in loblolly pine because of its importance in the paper industry (Zobel and Talbert, 1984).

BIOMASS PARTITIONING RESPONSES TO OZONE

In 1987, the greatest reduction in shoot biomass accumulation was in the needles, whereas by 1988 the reduction in stem + branch biomass accumulation was about the same as in needles, and by the end of the third yr the greatest reduction in shoot biomass accumulation was in stems and branches (Figure 2a). In 1987, the greatest percentage reduction in biomass accumulation by twice-ambient O₃ was in the roots (15.3 vs 13.4% in the shoots). At the end of the second yr percentage reduction in biomass accumulation was evenly distributed across above and belowground plant tissues (11.3 in roots vs 11.4% in shoots). By 1989, the 1987 pattern was repeated with the greatest reduction in biomass accumulation occurring in the roots (10.6 vs 7.4% in the shoots). The greatest reduction in root biomass accumulation in response to twice-ambient O₃ in 1987 was in coarse roots, whereas in 1988 and 1989 the greatest reductions were in the fine roots. Reduced C partitioning to roots is hypothetically caused by increased C retention in needles of O₃-exposed seedlings for repair of tissue damaged by O₃ (Tingey and Taylor, 1982; McLaughlin and Shriner, 1980). This hypothesis was supported in this study by the biomass data and by the finding that root respiration rates per gram of root tissue were reduced in the seedlings exposed to twice-ambient O₃ (Edwards, 1991).

RESPONSES TO RAINFALL CHEMISTRY

Net growth response to rainfall chemistry was small and not statistically significant for most plant tissues, but a trend of progressively decreasing net growth in the seedlings exposed to the lower pH rainfall compared to those exposed to the higher pH rainfall was evident over the 3-yr study period (Figure 2b). This trend was observed for all tissue types and was statistically significant by 1989 for branches ($P = 0.085$) with a 7% decrease in biomass accumulation and for coarse roots ($P = 0.053$) with a 2% decrease in biomass accumulation. We propose that the difference in timing of the rainfall chemistry responses and the O_3 responses may have been caused by difference in the modes and sites of action of the two treatments. Ozone effects may have been more direct (i.e., foliar membrane damage) and therefore more immediate than the rainfall chemistry effects (i.e., rainfall chemistry may have caused subtle changes in the soil chemistry resulting in delayed plant responses).

There were no effect of rainfall chemistry on height and diameter of the seedlings.

RESPONSES TO SOIL MAGNESIUM STATUS

Soil Mg status had no direct effect on total plant or major individual tissue biomass accumulation in loblolly pine (Figure 2C). Responses to the soil Mg treatments occurred only in the second foliage flush of the last yr of the study. In 1989 the seedlings grown in soil having $15 \mu\text{g Mg g}^{-1}$ had 7% less ($P = 0.053$) mass in the second needle flush than the seedlings grown in soil having $35 \mu\text{g Mg g}^{-1}$. A similar, but not statistically significant, response to soil Mg status was observed for the last two foliage flushes of 1988 and the third needle flush in 1989. However, the relatively large differences in these needle flushes had little effect on total needle mass in either 1988 or 1989 because they made up only about 1% of the total needle mass. No significant responses in biomass accumulation to soil Mg treatments were observed in any of the other plant tissues.

There were no effects of soil Mg status on the height and diameter of the seedlings.

4. Summary

Net growth of loblolly pine seedlings was reduced by ambient and above-ambient O_3 concentrations during each of the 3 yr of the study with the greatest growth reductions occurring during the yrs of greatest O_3 exposure levels. This response occurred with no evidence of visible needle damage or effects on pigment concentrations. The effects of O_3 on biomass accumulation was relatively uniform across all major plant tissue types. However, during the first and third yr of the study there was slightly greater O_3 induced reductions in biomass accumulation in belowground tissues than in aboveground tissues. There was also evidence that stem tissue density was less in plants exposed to twice-ambient O_3 concentrations.

Whereas O_3 responses were observed early (during the first yr of the study) and continued throughout the study, rainfall chemistry effects on biomass accumulation

were small by comparison and were not observed at statistically significant levels until the third yr of the study. Interactive effects of rainfall chemistry and soil Mg status were observed the third yr of the study with the greatest reduction in biomass accumulation occurring in the roots of seedlings exposed to both the low pH rainfall treatment and the low soil Mg treatment.

We propose both direct adverse effects of near ambient concentrations of tropospheric O₃ and indirect and slower acting interactive adverse effects of rainfall chemistry and soil nutrient status on the growth of loblolly pine in the southeastern U.S. The responses of loblolly pine to near ambient O₃ and near ambient rainfall chemistry (i.e. for the southeastern U.S.) are subtle and therefore difficult to detect. Nevertheless, the responses could be significant economically and ecologically.

Acknowledgments

This research was a joint activity conducted under the TVA/ORNL Cooperative Forest Studies Program with funding provided by the Electric Power Research Institute under Interagency Agreement No. TVA 1601-A1 with the U.S. Department of Energy under contract DE-AC05-84OR21400 with Martin Marietta Energy Systems, Inc. The authors gratefully acknowledge the technical assistance of Paul A. Mays and Tom Grizzard. We are also grateful to Dr. John J. Beauchamp for assistance with statistical analysis of the data and for aid in development of the experimental design. We acknowledge the technical contributions of the Roane State Community College students involved in this project.

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