THE CHRONIC RESPONSE OF YELLOW-POPLAR AND EASTERN WHITE PINE TO OZONE AND ELEVATED CARBON DIOXIDE: THREE-YEAR SUMMARY

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Abstract: The objective of this study was to determine the long-term effects of ozone (O_3) and carbon dioxide (CO_2) on the growth and physiology of eastern white pine *(Pinus strobus)* and yellow-poplar (*Liriodendron tulipifera*) under plantation conditions. Two separate plantations of each species were established in Delaware, Ohio, in 1991 and 1992. Seedlings were fumigated from mid-May to mid-October in 1992, 1993, and 1994 in standard 3m diameter open-top chambers. The treatments, each replicated three times in a randomized block design, included charcoal-filtered air (CF), 1X ambient O_3 (1X), 2X ambient O_3 (2X), 2X ambient ozone plus 350 ppm CO_2 above ambient (2X+CO_2), and open-air (OA) chamberless plot. Monthly growth and physiological measurements taken during each growing season included stem height and basal diameter, photosynthesis, stomatal conductance, chlorophyll content, and foliar nitrogen and phosphorus concentration. Subsamples of yellow-poplar were destructively harvested in 1993. First-season exposure to O_3 plus CO_2 appeared to have a stimulatory effect on the growth of both species. In 1993, decreases in white pine height growth, though not significant, were observed for both 2X- and 2X+CO_2-grown seedlings. Biomass and growth stimulations were observed on yellow-poplar in 1993, with mean increases of 14 percent in stem diameter and 16 percent in total plant height of yellow-poplar grown in 2X+CO_2 compared with all other treatments. Although not statistically significant at $p = 0.05$, 2X+CO_2-grown yellow-poplar had greater leaf, stem, branch and root biomass, and total leaf area compared with all other treatments. No significant effects on the growth of white pine were observed. However in late August 1994, both total height and basal stem diameter of 2X+CO_2-grown yellow-poplar were 21 percent greater than for all other treatments. The slower growing white pine appears to be responding differently to O_3 plus CO_2 than yellow-poplar.

INTRODUCTION

In the majority of studies of the response of tree species to air pollutants, potted seedlings have been exposed to gaseous pollutants under controlled environmental conditions for one to two growing seasons. Extrapolating data on seedlings to older trees is problematic as there is very little information on the response of older trees to gaseous pollutants. Experimental approaches that have been used in scaling seedling pollutant response to older trees include the use of whole-tree or branch chambers on mature trees (Albaugh et al. 1992; Grulke and Miller 1994; Hanson et al. 1994; Heagle et al. 1989; Houpis et al. 1991; Samuelson 1994; Teskey et al. 1991); descriptive physiological studies comparing mature and sapling trees along environmental gradients (McLaughlin et al. 1990); vegetative propagation of "mature" tissue (Rebbeck et al. 1992, 1993a); and free-air chamberless exposure systems (McLeod and Baker 1988). None of these approaches is without some limitations. To date, no research group has investigated the long-term effects of exposing the same population of trees to gaseous pollutants during their development from seedlings to saplings to older trees.

In this paper I summarize major findings of the first three years of long-term exposure of two important eastern tree species, yellow-poplar (*Liriodendron tulipifera*) and eastern white pine (*Pinus strobus*), to O_3 and elevated CO_2. The growth and physiological responses of these two field-planted species were studied within open-top chambers. Soil fertility was not manipulated and applications of irrigation water and pesticides were minimal. Three hypotheses were tested: (1) CO_2 enrichment ameliorates the negative effects of O_3; (2) the relative response to O_3 and CO_2 is the same in short-term studies with seedlings as with older trees; and (3) faster growing hardwood species are more sensitive to O_3 and more responsive to elevated CO_2 than slower growing conifer species.

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METHODS

In 1991, two separate but adjoining field plantations of yellow-poplar and white pine were established at the Northeastern Forest Experiment Station Forestry Sciences Laboratory at the USDA Forest Service in Delaware, Ohio, by clearing a 26- by 73-m area in a 20-year-old abandoned American elm (*Ulmus americana*) plantation. Within each plot, 12 plants were arranged in a circular pattern approximately 1.8 m in diameter. The white pine plantation consisted of seedlings from two sources: (1) northern genotype (2-0 stock) from the Upper Peninsula of Michigan (Baraga County), obtained from Dr. David Karnosky, Michigan Technological University, Houghton; and (2) southern genotype(1-0 stock) from northern Ohio (near Toledo), obtained from the State Nursery of Ohio, Marietta. Six seedlings of each source were planted within each plot. The yellow-poplar seedlings were planted on 7 May 1992, with 1-0 stock obtained from a private nursery in western Pennsylvania. Seed collections were made in southeastern Tennessee. A standard 3m diameter open-top chamber (Heagle et al. 1973) was placed over each plot after planting. No fertilizer was applied to either species. Since ambient rain was not excluded from the chambers, rain shadows sometimes resulted in the uneven distribution of water. This was corrected by supplemental watering. The frequency and duration of these waterings were based on the amount and distribution of ambient rainfall in the open-top chambers.

The study design consisted of a randomized complete block with three replications of the following treatments: charcoal-filtered air (CF); ambient O_3 concentration (1X); two times ambient O_3 concentration (2X); two times ambient O_3 concentration plus 350 ppm CO_2 above ambient (2X+CO_2); and open-air, chamberless plot (OA). The O_3 and CO_2 were dispensed automatically 24 h per day from mid-May through mid-October in 1992, 1993, and 1994. In 1994, the yellow-poplar open-top chambers were modified to increase their height to 4.6 m.

Monthly growth and physiological measurements taken during each growing season included stem height and basal diameter, photosynthesis, stomatal conductance, chlorophyll content, and foliar nitrogen and phosphorus concentration. Gas exchange rates for individual yellow-poplar leaves (node 6 to 8 or node 10 to 12 from the apex) or two sets of white pine fascicles (current-year or one-year-old needles) were measured with a LI-COR 6200 portable photosynthesis system[2]. From these same leaves, chlorophyll was extracted from 15mm diameter discs with dimethyl sulfoxide (Rebbeck et al. 1993a). The remaining leaf tissue was digested with sulfuric acid, potassium sulfate, and copper sulfate and quantified with a Lachat QuikChem Series 4000 Automated Ion Analyzer (Lachat 1992 a, b). Subsamples were taken to assess treatment impacts on leaf ultrastructure and spectral reflectance and transmission (Carter et al. 1995; McQuattie and Rebbeck 1994). Reflected and transmitted radiances were measured with an integrating sphere (LI-COR LI-1800UW spectroradiometer with LI1800-12S integrating sphere) (Carter et al. 1995). In late September 1993, shoot systems of six yellow-poplar seedlings from each chamber were destructively harvested and leaf area and leaf and stem dry mass determined. Root systems were excavated from a fixed volume (15,625 cm^3) of soil immediately surrounding the decapitated seedling and separated into tap and lateral roots. Senescent leaves harvested in October 1993 were packed in litter bags and placed in the forest floor in a hardwood stand at the Delaware Lab. Loss of leaf dry mass over time was compared among treatments (Boerner and Rebbeck 1995).

Pre-exposure stem height was used as a covariate in the statistical analysis of both the yellow-poplar and white pine growth data sets. A General Linear Model (GLM) (SAS 1988) procedure was used to test for significant treatment effects. A Least Significant Difference (LSD) means comparison test was performed on the covariate-adjusted means only when significant effects were found in the GLM analysis. The white pine data were analyzed as a split-plot design with treatment as a main plot and genotype-source as a subplot. Each monthly measurement data set was analyzed separately.

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Details on plant culture and maintenance as well as treatment dispensing and monitoring are reported elsewhere (Rebbeck 1993).

RESULTS AND DISCUSSION

The cumulative ozone dose for each of the three exposure seasons (1992-1994) is shown in Figure 1. Actual ozone levels for the 2X ambient ozone treatment were 1.3X, 1.6X, and 1.4X in 1992, 1993, and 1994, respectively.

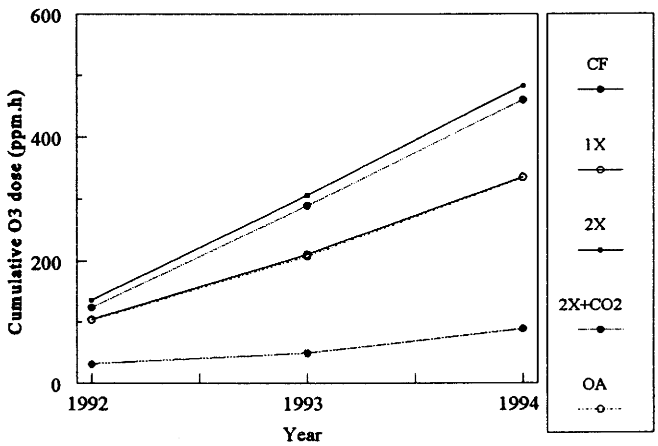

Figure 1. Cumulative ozone dose (ppm.h) of yellow-poplar grown in open-top chambers in 1992-94. The dose for white pine was comparable.

Yellow-poplar. Stimulated growth of yellow-poplar exposed to 2X+CO_2-air was observed during the three seasons of exposures (Table 1). In September 1992, stem diameter of yellow-poplar grown in 2X+ CO_2 was 13, 21, and 16 percent greater than that of CF-, 1X-, and 2X-grown trees, respectively ($p \leq 0.05$). In September 1993, yellow-poplar stem diameter (that portion of the terminal stem produced in 1991, 1992, or 1993) significantly increased from 10 to 17 percent when grown in 2X+CO_2-air compared with all other treatments ($p \leq 0.05$) (Rebbeck et al. 1993b). Total height growth also was 14-18 percent greater in yellow-poplar grown in 2X+CO_2-air compared with other treatments ($p \leq 0.05$). In late August 1994, both total height and basal stem diameter of 2X+CO_2-grown yellow-poplar were 21 percent greater than for all other treatments. Further, 2X+CO_2-grown yellow-poplar tended to have greater leaf, stem, branch and root biomass, and total leaf area compared with all other treatments when harvested in September 1993; p-values ranged from 0.18 to 0.78 (Table 2) (Rebbeck and Scherzer 1994).

Table 1. Yellow-poplar total stem height and basal diameter in 1992, 1993, and 1994.*

	Total Stem Height			Basal Diameter		
Treatment	1992	1993	1994	1992	1993	1994
		(cm)			(mm)	
CF	94.85 ± 3.14a	274.97 ± 10.36a	365.9 ± 20.8a	9.85 ± 0.5a	13.99 ± 0.78a	45.17 ± 2.73a
$1XO_3$	90.84 ± 4.44a	267.35 ± 8.66a	343.9 ± 20.2a	8.93 ± 0.5a	29.24 ± 1.39a	39.46 ± 3.37a
$2XO_3$	96.89 ± 4.08a	285.44 ± 8.43a	382.2 ± 24.3a	9.47 ± 0.5a	29.71 ± 1.17a	43.85 ± 2.98a
$2XO_3+CO_2$	102.88 ± 5.04b	304.70 ± 10.47b	460.0 ± 11.1b	11.33 ± 0.5b	34.41 ± 1.61b	53.94 ± 3.18b

*Each value is a mean of 36 trees ± one standard error. Means followed by different letters are significantly different at $p < 0.05$.

Table 2. Yellow-poplar biomass (g dry wt) harvested in September 1993.

Treatment	Leaves	Branches	Primary stem	Root
CF	212.1 ± 27.1 a	122.2 ± 19.3 a	284.9 ± 34.2 a	120.1 ± 10.6 a
$1XO_3$	227.6 ± 38.8 a	126.3 ± 28.4 a	287.2 ± 51.9 a	110.3 ± 12.2 a
$2XO_3$	215.9 ± 18.7 a	121.1 ± 15.1 a	280.4 ± 28.3 a	113.2 ± 10.1 a
$2XO_3+CO_2$	231.2 ± 25.4 a	139.7 ± 16.5 a	356.0 ± 54.0 a	136.7 ± 10.0 a

Each value is mean of 36 trees ± one standard error. Means followed by different letters are significantly different at $p < 0.05$.

White pine. No significant growth effects attributable to O_3 or O_3 plus CO_2 were observed for white pine in any of the three growing seasons (Table 3). In September 1992, height growth of white pine in 2X+CO_2-air was 50 and 18 percent greater than for the CF- and 2X-air treatments, respectively ($p = 0.08$) (Rebbeck 1993; Rebbeck et al. 1993a). In September 1993, height growth was lower for both 2X- and 2X+CO_2-grown seedlings than for seedlings of other treatments (Rebbeck and Scherzer 1994). The two seed sources grew differently, but no genotype X treatment interactions were observed at any time.

Table 3. Stem height growth and basal diameter of white pine in 1992, 1993, and 1994.*

	Stem Height Growth			Basal Diameter		
Treatment	1992	1993	1994	1992	1993	1994
		(cm)			(mm)	
CF	3.83 ± 1.54a	27.46 ± 2.60a	49.53 ± 3.00a	8.71 ± 0.37a	16.54 ± 0.87a	27.27 ± 1.25a
$1XO_3$	4.99 ± 1.55a	26.50 ± 3.23a	45.06 ± 2.65a	8.53 ± 0.39a	14.68 ± 0.90a	25.81 ± 1.23a
$2XO_3$	6.32 ± 1.56a	24.13 ± 2.48a	47.93 ± 3.14a	8.94 ± 0.47a	15.94 ± 0.98a	26.56 ± 1.42a
$2XO_3+CO_2$	7.68 ± 1.54a	20.16 ± 2.61a	50.07 ± 3.92a	8.91 ± 0.46a	15.59 ± 1.25a	30.46 ± 2.03a

*Each value is mean of 36 trees ± one standard error. Means followed by different letters are significantly different at $p < 0.05$.

Physiological Effects

Yellow-poplar. Impacts of O_3 and O_3 plus CO_2 on seasonal photosynthetic rates of yellow-poplar at saturating light were observed in 1992 and 1993 (Table 4). Additions of enriched CO_2 to twice ambient O_3 ameliorated reductions in net photosynthesis caused by O_3. In 1992, net photosynthesis was reduced by 34 percent by 2X-air and increased by 13 percent by 2X+CO_2-air compared with CF-grown trees. In 1993, 2X+CO_2 increased net photosynthesis by 31 to 45 percent compared with all other treatments. In both 1992 and 1993, respiration rates were approximately 36 percent higher in leaves of yellow-poplar trees grown in 2X O_3-air than in leaves of CF-grown trees; CO_2 enrichment to 2X O_3 had no additional effect on respiration rates. In 1992, stomatal conductance was reduced by 7 and 32 percent in 2X O_3- air and 2X+CO_2 -air, respectively, compared with CF-air. In July 1993, stomatal conductance rates of 2X+CO_2-grown yellow-poplar were 20 to 45 percent lower than for all other treatments.

Table 4. Seasonal photosynthetic rates ($\mu mol\ CO_2 m^{-2} s^{-1}$) of yellow-poplar and white pine in 1992 and 1993 at saturating light.

	Yellow-poplar		White Pine	
Treatment	1992	1993	1992	1993
CF	13.07 ± 1.77a	6.94 ± 4.83a	6.85 ± 2.06a	9.95 ± 1.77a
$1XO_3$	11.86 ± 1.44a	8.79 ± 3.29a	7.04 ± 1.69a	9.11 ± 1.99a
$2XO_3$	8.61 ± 1.25b	8.12 ± 3.93a	7.90 ± 1.89a	9.68 ± 2.19a
$2XO_3+CO_2$*	14.82 ± 1.88a	12.69 ± 3.44b	6.30 ± 0.71a	30.74 ± 1.65b

* Measurements at 700 ppm CO_2 for $2XO_3+CO_2$ versus 350 ppm CO_2 for other treatments. Values are means across sampling dates, leaf or needle age, and genotype (white pine only). Means followed by different letters are significantly different at $p < 0.05$.

In 1992, total chlorophyll content was 21 and 30 percent lower in leaves of yellow-poplar grown in 2X- and $2X+CO_2$-air, respectively, than in those grown in CF-air. In 1993, total chlorophyll content was reduced by 33 percent in $2X+CO_2$-air compared with all other treatments (Rebbeck et al. 1995). Total chlorophyll content was reduced by exposure to 2X O_3 only in older yellow-poplar leaves. In 1993, foliar nitrogen of yellow-poplar was reduced by 32 to 38 percent in $2X+CO_2$-air compared with all other treatments; O_3 alone did not affect foliar nitrogen content in 1993 (Scherzer and Rebbeck 1995).

Litter decomposition of yellow-poplar leaves was not affected by O_3, but $2X+CO_2$-grown leaves had 34 to 43 percent less decay than leaves of other treatments. These findings imply that the C:N ratio of the forest floor and soil would be raised and nitrogen limitations exacerbated by elevated CO_2.

In both 1992 and 1993, the cuticular membrane ultrastructure of yellow-poplar leaves was altered both by O_3 and elevated CO_2. McQuattie and Rebbeck (1994) reported that the cuticular membranes of 2X O_3-grown yellow-poplar leaves were 64 and 36 percent thinner than those of seedlings grown in CF-air and $2X+CO_2$-grown, respectively, ($p = 0.01$). In July and August of 1994, cuticle membranes were thickest in $2X+CO_2$-grown yellow-poplar leaves; CF-grown cuticles were intermediate and 2X O_3-grown were the thinnest. We hypothesize that the some of the extra carbon assimilated by the O_3 plus CO_2-grown trees was used to produce the cuticular membrane.

White pine. In 1992 and 1993, O_3 alone did not have a negative effect on the photosynthetic rates of white pine needles (Table 4). Stimulations in net photosynthesis of white pine grown in $2X+CO_2$-air were not observed until late August 1992. In 1993, photosynthetic rates of current- and 1-year-old needles of trees grown in $2X+CO_2$-air increased by 57 to 80 percent compared with all other treatments ($p = 0.01$).

In 1993, total chlorophyll content of 1-year-old white pine needles grown in $2X+CO_2$-air was reduced 41-52 percent compared with other treated trees in 1993 (Rebbeck et al. 1995). Current-year white pine needle total chlorophyll content was not affected by 2X- or $2X+CO_2$-air.

The leaf optical properties of white pine and yellow-poplar exposed to O_3 and O_3 plus CO_2 were monitored in 1992 (Carter et al. 1995). Ozone increased leaf reflectance and transmittance and decreased leaf absorptance in yellow-poplar. CO_2 added to 2X O_3 did not affect reflectance but decreased transmittance and increased absorptance within the range of 400 to 421 nm and increased transmittance and decreased absorptance in the 694 to 697 nm range. In white pine, 2X O_3 increased reflectance in the 537 to 647, 650, and 691 to 716 nm ranges. Transmittances and absorptances were not determined for white pine. The observed spectral responses were explained primarily by decreased concentrations of chlorophyll *a* as has been the case with a number of plant stressors.

SUMMARY AND CONCLUSIONS

In this three-year study, O_3 alone had no significant effect on the growth of eastern white pine or yellow-poplar. A fast-growing indeterminate hardwood species, yellow-poplar appeared more responsive to additions of CO_2 to O_3 than the slower growing determinate conifer. Yellow-poplar exhibited the typically reported responses to enriched CO_2 including increased height and diameter growth, increased shoot and root biomass production, increased photosynthesis, decreased stomatal conductance, decreased total chlorophyll and foliar nitrogen content, and decreased litter decomposition rate, even in the presence of up to 1.6X ambient O_3 (target was $2XO_3$). Leaf gas exchange along with growth, biomass production, and foliar nutrient dynamics will continue to be monitored to determine if acclimation of yellow-poplar to elevated CO_2 occurs in the presence of O_3.

Although white pine exhibited increased rates of photosynthesis and decreased total chlorophyll content in response to 2X O_3 plus enriched CO_2, impacts on whole-tree growth were not observed. And although the initial growth of this white pine population was slow, it is possible that these now well-established trees will begin to exhibit more typical growth effects due to enriched CO_2.

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