New Phytol. (1990), **116**, 689–694

Growth of five families of *Pinus taeda* L. during three years of ozone exposure

BY M. B. ADAMS[1], J. M. KELLY[2], G. E. TAYLOR, JR.[3] AND N. T. EDWARDS[4]

[1] *USDA Forest Service, Timber and Watershed Laboratory, Parsons, WV* 26287, *USA*
[2] *Tennessee Valley Authority, Cooperative Forest Studies Program, P.O. Box 2008, Oak Ridge, TN 37831-6038, USA*
[3] *Biological Sciences Center, Desert Research Institute, P.O. Box 60220, Reno, NV 89506-0220, USA*
[4] *Environmental Sciences Division, Oak Ridge National Laboratory, P.O. Box 2008, Oak Ridge, TN 37831-6038, USA*

(*Received 17 April 1990; accepted 20 August 1990*)

SUMMARY

Loblolly pine (*Pinus taeda* L.) seedlings of five half-sib families were grown for 3 yr in the field in open-top chambers. The seedlings were fumigated during the growing seasons (approximately April–October) with ozone at the following target levels: subambient (CF), ambient (AMB), and ambient + 60 ppb (AMB +). At the end of the three growing seasons, no significant ozone effects on diameter, height or total biomass of the seedlings were detected, and no statistically significant ozone-family interactions were detected. Analysis of growth trends suggest that drought during the second and third growing seasons may have interacted with the ozone treatments. The importance of long-term studies under realistic field conditions is discussed.

Key words: Ozone, loblolly pine, genotypic variations, drought effects.

INTRODUCTION

Considerable concern has been expressed in recent years about the potential relationships between changes in the chemical climate and reported or hypothesized alterations in forest growth. Elevated ozone concentrations, once considered largely an urban problem, have now become ubiquitous even in seemingly remote rural areas (Meagher *et al.*, 1987; Pinkerton & Lefohn, 1987). In his recent review of the impacts of ozone on forest species, Pye (1988) noted that current ambient levels of ozone are sufficient to reduce seedling growth and photosynthesis in the majority of the 43 species he surveyed. Seedling response to ozone at ambient and near-ambient concentrations appears to be a complex interaction of a number of factors, both biotic and abiotic, with time (length of exposure) being an important variable. The importance of exposure duration is illustrated by the 5-month study of Jensen (1973), where an array of responses was observed, including stimulation followed by reduction and reduction followed by recovery. Had Jensen (1973) chosen to terminate his study at any given point during the five months, a variety of 'final' results could have been reported. In addition, of the 25 studies of tree species reviewed by Pye (1988), only the studies of Chevone, Skelly & Yang (1983) and Wang, Bormann & Karnosky (1986) exceeded a year in length while the great majority of study periods were in the 30- to 90-d range.

Length of exposure becomes an even more important consideration with coniferous species, since the function of retained needles in subsequent growing seasons may be influenced by past exposure history. Likewise, as a seedling ages, carbon allocation patterns and the relative proportion of photosynthetic to non-photosynthetic tissue change in response to genetic and environmental considerations. The potential importance of genetic or genotypic differences within a species influencing plant response to an air pollutant was clearly illustrated by the early work of Berry (1964) on eastern white pine (*Pinus strobus*). Recent work by McLaughlin *et al.* (1988), Shafer & Heagle (1989), and Adams, Kelly & Edwards (1988) also provides evidence of a genotype × ozone interaction for loblolly pine (*Pinus taeda* L.).

In designing the study reported here, it was determined that the influence of these two factors, time and genotype, would be integral parts of the work to be done. Loblolly pine was chosen for study because of its economic importance and broad geographic distribution within a region of the United States that consistently reports elevated ozone concentrations. Additionally, growth declines in southern pines have been observed (Sheffield *et al.*, 1985), with elevated ozone being one of the most frequently hypothesized causal agents (McLaughlin, 1985). The work reported here evaluated the growth and biomass response of seedlings of five families of loblolly pine over three growing seasons to ambient, subambient, and above-ambient levels of ozone under controlled field conditions using open-top chambers. The objectives were to determine if there is a differential response to ozone among the genotypes selected in this study and to determine if any observed differences were consistent through time.

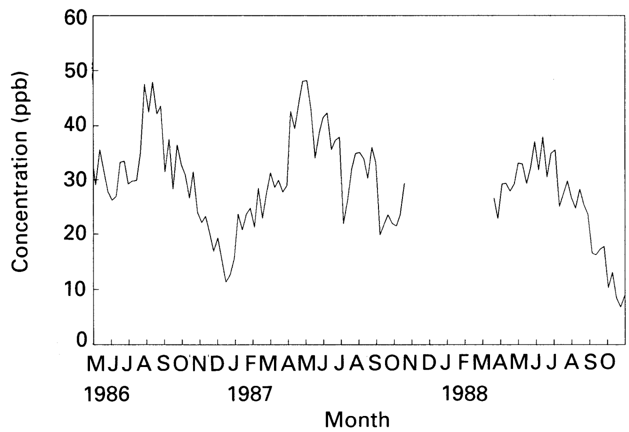

Figure 1. Mean weekly ambient ozone concentrations at Air Pollution Effects Field Research Facility, 1986–8. Data for November 1987 until March 1988 are not available.

MATERIALS AND METHODS

Seedling origin and establishment were detailed by Adams *et al.* (1988). Six-month-old seedlings from five half-sib families of loblolly pine were transplanted into 24 l pots containing 18 kg (oven-dry equivalent) of sieved soil collected from the A horizon of a fine, loamy silicious, mesic typic Hapludults. The A horizon was selected because it is

Table 1. *Growing season ozone exposure statistics (ppb) by treatment, 1986–8*

	CF			AMB			AMB+		
	7 h mean*	24 h mean	1 h max	7 h mean	24 h mean	1 h max	7 h mean	24 h mean	1 h max
1986									
May	28	21	49	56	41	91	95	71	201
June	27	22	74	55	41	101	101	79	193
July	23	19	34	56	38	102	106	72	194
Aug.	22	18	33	58	40	102	112	79	209
Sept.	21	17	54	46	33	102	82	61	202
Oct.	18	16	29	39	30	69	66	41	130
1987									
May	36	28	65	61	46	99	117	104	169
June	35	26	62	60	42	109	116	101	171
July	33	23	71	58	37	106	103	80	181
Aug.	32	22	57	61	40	99	117	97	157
Sept.	26	19	57	47	31	105	94	81	169
Oct.	26	20	73	40	30	83	78	53	133
1988									
March	28	22	58	43	35	66	42	34	65
April	30	23	65	48	37	93	65	57	207
May	39	25	71	65	42	107	90	65	274
June	40	25	76	73	44	122	89	62	148
July	32	20	82	60	36	130	80	57	195
Aug.	33	21	87	58	33	110	89	66	178
Sept.	25	19	60	46	29	105	85	89	172
Oct.	34	23	88	60	38	130	82	62	274

* 7 h, mean, 10·00–17·00 h.

naturally low in exchangeable magnesium content, which was an important factor in the large companion study (Edwards *et al.*, 1990). These five families were selected for this study because they have been successfully outplanted in the region where the study was conducted, which is located at the northern end of the natural range of loblolly pine. Seven seedlings of each family were then placed into each of nine open-top exposure chambers at the Oak Ridge National Laboratory Air Pollution Field Research Facility in June 1986. Seedlings were exposed to one of three ozone treatments during three growing seasons (approximately April–October, 1986–8). Treatments included ambient ozone (AMB); subambient ozone [charcoal-filtered air, approximately 60% of ambient (CF)]; and above-ambient ozone [target concentration of ambient ozone + 60 ppb ozone (AMB +)]. Each treatment was replicated three times, using a completely randomized design. Ozone generation and delivery were described by Adams *et al.* (1988) and McEvers, Bowers & Edwards (1988). Ambient ozone concentrations and exposure statistics for the three years are given in Figure 1 and Table 1. Note that mean target levels of 60 ppb above ambient were not achieved in 1988, and that ambient ozone concentrations were relatively lower in 1988. Seedlings received ambient precipitation during the study (Fig. 2) except under extreme drought conditions when they were watered to ensure survival. Symptoms of water stress were observed despite this supplemental watering, probably due to the small soil volume of the pots in which they were growing.

Diameter and height were measured periodically on the same subset of 90 trees over the 3 yr study period. At the end of each growing season, two seedlings per family were harvested from each chamber, for a total of 90 seedlings. Due to seedling mortality, 89 seedlings were harvested in 1987 and 1988. Plants were separated into foliage, stem, fine roots (< 1 mm diameter), and coarse roots (> 1 mm diameter) for biomass measurements (oven-dry weight basis).

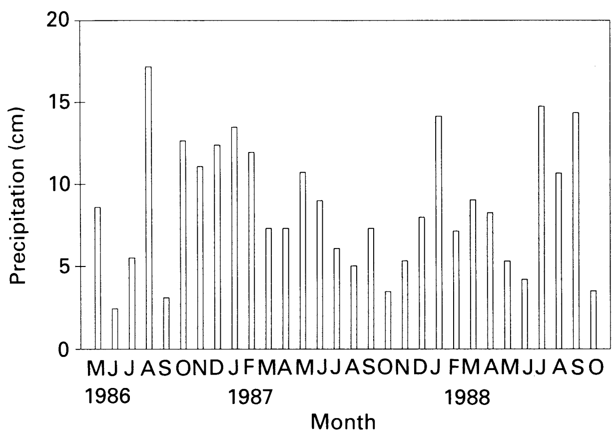

Figure 2. Ambient precipitation at Air Pollution Effects Field Research Facility, 1986–8.

Analysis of covariance was used to evaluate the data. Main effects were ozone treatment and family, with family a fixed effect. Chamber was nested within ozone treatment (random effect) and the interactions were family × ozone and family × chamber (ozone). Initial D^2H (diameter squared × height) was used as the covariate to account for initial differences in seedling sizes. Ozone treatment and family means were compared and significance evaluated at the $P = 0{\cdot}05$ level of significance unless otherwise stated (SAS Institute, Inc., 1985). Height and diameter data were evaluated using analysis of repeated measures (Morrison, 1976) to examine treatment and growth patterns over time.

RESULTS AND DISCUSSION

The major effects of the treatments were on foliar biomass during the first two years. At the end of these two growing seasons, foliar biomass of the AMB seedlings was significantly greater than that of CF or AMB + seedlings (Table 2). No significant effects on foliar biomass were detected in 1988. Total seedling biomass was also the greatest for the AMB seedlings, although differences were not always statistically significant. No visible symptoms of damage were observed after 3 yr, nor did mass of dead foliage increase significantly as a result of ozone fumigation (data not shown). A trend toward earlier senescence was observed during the first of this year study (Adams *et al.*, 1988).

Other researchers have reported reduced above-ground growth of some loblolly pine families at ambient ozone levels (McLaughlin *et al.*, 1988; Shafer & Heagle, 1989). In the present study, the opposite was observed; seedlings grown with charcoal-filtered air were consistently smaller than those grown with ambient ozone levels. It was expected that, if ozone produced a significant negative effect on growth, seedlings grown with the highest ozone levels (AMB +) would be smaller than those receiving ambient ozone concentrations (AMB). However, this was not observed in this study. It was hypothesized (Adams *et al.*, 1988) that the observed pattern might be an artifact of higher N deposition in the AMB + chambers due to production of NO_x during ozone generation from ambient air (Harris *et al.*, 1982), or to differential N nutrition resulting from effects of charcoal-filtration (Roberts, Brown & Blank, 1988). Subsequent measurements of gaseous N deposition do not provide support for these hypotheses. The maximum contribution of N from these two sources in the AMB + treatment was estimated to be < 6% of total plant N (G. E. Taylor, unpublished data). Because this represents a maximum value, an ameliorative effect due to additional N is unlikely.

Table 2. *Mean biomass (g dry weight) of* Pinus taeda *seedlings (across five families) over three growing seasons by treatment. Means and standard deviations are given*

Year	Treatment	Foliage	Stem	Fine roots	Coarse roots	Total biomass
1986	CF	7·0 ± 2·1 a*	3·7 ± 1·0 a	3·2 ± 0·8 a	2·7 ± 0·8 a	17·3 ± 4·1 ab
	AMB	8·2 ± 1·6 b	3·7 ± 0·8 a	3·4 ± 0·6 a	2·9 ± 1·0 a	19·0 ± 2·5 a
	AMB+	6·6 ± 1·5 a	3·5 ± 0·8 a	3·4 ± 0·7 a	2·4 ± 0·7 a	16·5 ± 2·9 b
1987	CF	37·5 ± 5·2 a	21·9 ± 4·3 a	18·7 ± 4·8 a	13·6 ± 2·5 a	91·7 ± 12·4 a
	AMB	42·3 ± 4·2 b	26·3 ± 4·4 b	20·1 ± 4·2 a	15·0 ± 9·3 b	103·7 ± 9·3 b
	AMB+	39·4 ± 5·1 a	23·6 ± 3·5 a	17·0 ± 3·8 a	13·0 ± 2·7 a	93·1 ± 10·4 a
1988	CF	83·7 ± 8·6 a	53·1 ± 9·4 a	34·6 ± 8·5 a	35·3 ± 8·6 a	206·6 ± 24·2 a
	AMB	85·0 ± 10·8 a	55·5 ± 9·3 a	32·8 ± 8·8 a	37·5 ± 5·6 a	210·9 ± 22·8 a
	AMB+	81·1 ± 7·6 a	56·7 ± 6·8 a	31·9 ± 7·6 a	34·4 ± 6·3 a	204·2 ± 17·5 a

* Means within the same year and column followed by the same letter are not significantly different ($P = 0·05$).

Table 3. *Diameter, height, D^2H (diameter squared × height), by treatment for three growing seasons. (Mean ± standard deviation). All measurements represent end of the growing season (October) measurements*

Year	Treatment	Diameter (cm)	Height (cm)	D^2H (cm^3)
1986	CF	0·87 ± 0·07 a*	27·8 ± 5·1 a	21·4 ± 6·6 a
	AMB	0·86 ± 0·09 a	25·7 ± 4·5 a	19·8 ± 5·6 b
	AMB+	0·82 ± 0·07 a	25·7 ± 5·4 a	17·8 ± 5·6 b
1987	CF	1·53 ± 0·11 a	64·5 ± 9·2 a	152·7 ± 38·7 a
	AMB	1·52 ± 0·12 a	64·3 ± 6·6 a	151·2 ± 34·5 a
	AMB+	1·50 ± 0·11 a	66·2 ± 8·9 a	149·7 ± 31·9 a
1988	CF	2·11 ± 0·22 a	97·4 ± 14·8 a	444·6 ± 152·0 a
	AMB	2·14 ± 0·15 a	90·6 ± 12·1 a	416·1 ± 87·9 a
	AMB+	2·19 ± 0·16 a	99·2 ± 14·6 a	476·8 ± 101·4 a

* Means within the same year and column followed by the same letters are not significantly different ($P = 0·05$).

Analysis of repeated measures revealed a statistically significant measurement date × ozone interaction on diameter in 1987 and 1988, suggesting the relative effects of the ozone treatments on diameter had changed during the course of these two growing seasons (Table 3). This effect, most obvious during the 1988 growing season, is attributed to drought stress. Early in June of 1988 the seedlings experienced a severe drought stress (see Fig. 2), which differentially affected the diameter growth of the seedlings in the three ozone treatments (Fig. 3). It is hypothesized that the AMB+ treatment protected the seedlings from water stress because stomatal closure occurred earlier in the diurnal cycle (Barnes, 1972; Coyne & Bingham, 1981; Taylor *et al.*, 1989). This hypothesis is supported by the observation of Tjoelker, Luxmoore & Schwarz (1989) that water use efficiency increased slightly with increased ozone concentration in loblolly pine seedlings grown in the same chambers during the same year. In addition, a significant measurement date × ozone interaction was detected for both diameter and height in 1987, also believed to be due to drought stress. However, the drought stress occurred later in 1987 growing season and was not as severe as in 1988 (Fig. 2). The seasonal water use efficiency of the foliage of the AMB+ seedlings was estimated during 1987 through examination of stable isotope ratios in foliage from each of the treatments (Taylor *et al.*, 1989). These ratios were found to be

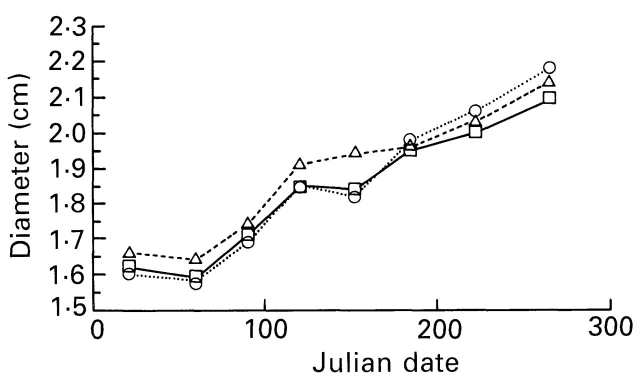

Figure 3. Diameter growth of seedlings of *Pinus taeda* by ozone treatment, 1988. □, Subambient; △, ambient; ○, ambient + 60 ppb.

Table 4. *Mean biomass (g) of* Pinus taeda *components by family (across ozone treatments) at the end of each of three growing seasons*

Year	Family	Foliage	Stem	Fine roots	Coarse roots	Total biomass
1986	1	7·06 a b*	4·08 a	3·58 a b	2·80 a	18·18 a
(n = 90)	2	6·35 b	3·54 a	3·37 a b	2·26 a	16·33 a
	3	7·52 a b	3·55 a	3·02 b	2·34 a	17·20 a
	4	7·89 a	3·49 a	3·70 a	2·95 a	18·61 a
	5	7·42 a b	3·51 a	3·12 a b	2·94 a	17·65 a
1987	1	39·80 a	24·53 a	18·24 a	13·98 a	96·56 a
(n = 89)	2	40·26 a	23·11 a	16·02 b	14·21 a	93·60 a
	3	40·53 a	24·61 a	18·91 a	14·20 a	98·24 a
	4	39·06 a	24·24 a	18·23 a	13·92 a	96·45 a
	5	39·12 a	23·20 a	20·44 a	13·24 a	96·01 a
1988	1	83·3 a	58·6 a	33·7 a	34·0 a	209·6 a
(n = 89)	2	85·9 a	52·0 b	33·2 a	36·5 a	207·6 a
	3	84·1 a	53·1 b	30·5 a	36·3 a	204·1 a
	4	80·3 a	61·2 a	33·8 a	37·9 a	213·3 a
	5	82·7 a	50·4 b	34·1 a	33·9 a	201·2 a

* Means within the same year and column followed by the same letter are not significantly different (P = 0·05).

statistically greater than in seedlings from the other two treatments. The measurements were not repeated for these seedlings in 1988, but similar results would be expected with 1988 foliage. Other researchers have also reported an apparent increase in drought tolerance at elevated ozone levels (Tingey & Hogsett, 1985).

It is important to note that the peak ambient ozone levels occurred during July in 1986, but occurred much earlier (April and May) in 1987 and 1988. Because of the indeterminate nature of loblolly pine growth, these differences could result in significant growth differences. For example, the first and generally largest growth flush occurs in the spring, with the second and third flushes occurring approximately every 40–60 d. Higher ozone concentrations early in the growing season could negatively affect the young, photosynthetically active foliage of the first flush, resulting in diminished photosynthate supply for elongation of later growth flushes. The cumulative effect could be less foliar biomass relative to that in seedlings exposed to elevated ozone after the initial flush had completed elongation. This experiment was not designed to test this hypothesis, nor has timing of exposure been studied extensively for indeterminate species such as loblolly pine.

Family differences were statistically significant for diameter, height, and D^2H during all three growing seasons, and for most biomass components in 1986, fine root biomass in 1987, and stem biomass in 1988 (Table 4). Family rankings were consistent over the three growing seasons and no significant family × ozone effects were detected except for foliar biomass after the first growing seasons, as reported by Adams *et al.* (1988). The lack of a significant interaction may be due to low statistical power, or to low variability among the genotypes. The genotypes appeared to vary in their relative responses in total root and total plant biomass to the ozone treatments (Table 5); however, these changes were not statistically significant. Shafer & Heagle (1989) reported a significant ozone × family interaction for four North Carolina full-sib families of loblolly pine, but the nature of the interaction varied with the plant parts measured. It is also possible that the five genotypes in the present study varied in drought tolerance, further confounding the relative stresses experienced by the plants. A statistically significant measurement date × family effect was detected for diameter, height, and D^2H during the 1988 growing season, providing some support for the hypothesis that a drought × family interaction may exist. This hypothesis cannot be tested with these data, however. No significant date × family × ozone interactions

Table 5. *Mean relative differences in biomass of 3-yr-old* Pinus taeda *seedlings by ozone treatment, compared to biomass of seedlings with charcoal-filtered air*

Family	Treatment	Root Biomass (%)	Total plant biomass (%)
1	AMB	−4·7	+0·7
	AMB+	−15·0	−3·6
2	AMB	+7·3	+7·6
	AMB+	+4·0	+3·2
3	AMB	+5·7	+3·0
	AMB+	−7·4	−2·0
4	AMB	−1·8	−0·9
	AMB+	−3·2	+0·4
5	AMB	−2·3	+2·5
	AMB+	+2·5	−0·3

were detected. Given the apparent strength of the genetic component of aboveground growth, it may be that the influence of the genotype on a plant's response to ozone stress may be muted as a function of other environmental factors that also influence ozone tolerance.

We hypothesize that the relative role of genotype in controlling resistance to ozone is strongly linked with other natural stress, in this case drought. Under other environmental stresses another environmental factor(s) could influence the observed response. For example, Tjoelker *et al.* (1989) reported an ozone × nitrogen interaction for loblolly pine growth, with higher ozone levels reducing growth response to N additions, and concluded that ozone effects on biomass partitioning of plants may be mediated by soil N supply. Loblolly pine genotypes may vary in their nutrient use efficiency. Thus, response to ozone by a particular genotype may also vary with soil N. We hypothesize that the pattern of ozone response among conspecifics will vary spatially (e.g. across regions) and temporally (e.g. seasonally and annually). These hypotheses further reinforce the need to evaluate ozone response in a realistic context of several interacting stresses over time and argue against conducting single factor studies in which all other environmental resources are maintained at an optimum.

ACKNOWLEDGEMENTS

Research sponsored by Tennessee Valley Authority Electric Power Research Institute under Interagency Agreement No. TVA 1610-1610-A1W with the U.S. Department of Energy under contract DE-AC05-840R21400 with Martin Marietta Energy Systems, Inc. This effort was a joint activity conducted under TVA/ORNL Cooperative Forest Studies Program.

REFERENCES

Adams, M. B., Kelly, J. M. & Edwards, N. T. (1988) Growth of *Pinus taeda* L. seedlings varies with family and ozone exposure level. *Water, Air and Soil Pollution* **38**, 137–150.

Barnes, R. L. (1972). Effects of chronic exposure to ozone on photosynthesis and respiration of pines. *Environmental Pollution* **3**, 123–138.

Berry, C. R. (1964). Differences in concentrations of surface oxidant between valley and mountaintop conditions in the southern Appalachians. *Journal of Air Pollution Control Association* **14**, 238–239.

Chevone, B. I., Skelly, J. M. & Yang, Y. S. (1983). The influence of ambient pollutants on the growth of seedling forest trees and native vegetation. *Aquilo Ser Botanica* **19**, 198–207.

Coyne, P. I. & Bingham, G. E. (1981). Comparative ozone dose response of gas exchange in a ponderosa pine stand exposed to long-term fumigations. *Journal of the Air Pollution Control Association* **31**, 38–41.

Edwards, N. T., Taylor, G. E., Jr., Adams, M. B., Simmons, G. L. & Kelly, J. M. (1990). Ozone, acidic rainfall and soil Mg effects on growth & foliar pigments of *Pinus taeda* L. *Tree Physiology* **6**, 95–104.

Harris, G. W., Carter, W. P. L., Winer, N., Graham, R. A. & Pitts, J. N., Jr. (1982). Studies of non-ozone species produced in a corona discharge ozonizer. *Journal of the Air Pollution Control Association* **32**, 274–276.

Jensen, K. F. (1973). Response of nine forest tree species to chronic ozone fumigation. *Plant Disease Reports* **57**, 914–917.

McEvers, J. A., Bowers, T. L. & Edwards, N. T. (1988). *Air Pollution Effects Field Research Facility. I. Ozone Flow Control & Monitoring System.* ORNL/TM-10758. Oak Ridge National Laboratory, Oak Ridge, Tennessee, USA.

McLaughlin, S. B. (1985). Effects of air pollution on forests: A critical review. *Journal of the Air Pollution Control Association* **35**, 516–534.

McLaughlin, S. B., Adams, M. B., Edwards, N. T., Hanson, P. J., Layton, P. A., O'Neill, E. G. & Toy, W. K. (1988). *Comparative Sensitivity, Mechanisms and Whole-Plant Implications of Responses of Loblolly Pine Genotypes of Ozone and Acidic Deposition.* ORNL/TM-10777. Oak Ridge National Laboratory, Oak Ridge, Tennessee, USA.

Meagher, J. F., Lee, N. T., Valente, R. J. & Parkhurts, W. J. (1987). Rural ozone in the southeastern United States. *Atmospheric Environment* **21**, 605–615.

Morrison, D. F. (1976). *Multivariate Statistical Methods*, 2nd Edn. McGraw Hill, New York.

Pinkerton, J. E. & LeFohn, A. S. (1987). The characterization of ozone data for sites located in forested areas of the eastern United States. *Journal of the Air Pollution Control Association* **37**, 1005–1010.

Pye, J. (1988). Impact of ozone on growth and yield of trees: a review. *Journal of Environmental Quality* **17**, 347–360.

Roberts, T. M., Brown, K. A. & Blank, L. W. (1988). Methodological aspects of the fumigation of forest trees with gaseous air pollutants using closed chambers. In: *Air Pollution and Ecosystems* (Ed. by P. Mathy), pp. 338–360. D. Reidel Publishing Company, Dordrecht.

SAS Institute Inc. (1985). *SAS User's Guide: Statistics*, Version 5 edition. SAS Institute, Cary, North Carolina, USA.

Shafer, S. R. & Heagle, A. S. (1989). Growth response of field-grown loblolly pine to chronic doses of ozone during multiple growing seasons. *Canadian Journal of Forest Research* **19**, 821–831.

Sheffield, R. M., Cost, N. D., Bechtold, W. A. & McClure, J. P. (1985). *Pine Growth Reductions in the Southeast.* USDA Forest Service, Resource Bulletin SE-83. Southeastern For. Exp. Stn., Asheville, North Carolina, USA.

Taylor, G. E., Jr., Gunderson, C. A., Tjoelker, M. G. & Adams, M. B. (1989). *Ozone and drought stress in* Pinus taeda *L.* (loblolly pine): *recognition of a Significant Interaction under Field Conditions using Stable Carbon Isotopes.* Technical Summary, Environmental Sciences Division. Oak Ridge National Laboratory, Oak Ridge, TN.

Tingey, D. T. & Hogsett, W. (1985). Water stress reduces ozone injury via a stomatal mechanism. *Plant Physiology* **77**, 944–947.

Tjoelker, M. G., Luxmoore, R. J. & Schwarz, O. J. (1989). *Soil Nitrogen and Ozone Effects on Growth, Physiology and Nutrition of Loblolly Pine and Yellow-popular Seedlings.* ORNL/TM-110665. Oak Ridge National Laboratory, Oak Ridge, Tennessee, USA.

Wang, D., Borman, F. H. & Karnosky, D. F. (1986). Regional tree growth reductions due to ambient ozone: evidence from field experiments. *Environmental Science & Technology* **20**(11), 1122–1125.