RESPONSE OF LOBLOLLY PINE SEEDLING GENETIC VARIATION TO OZONE

A. E. Wiselogel [1/]

Abstract.--Ozone was observed to be a significant source of variation for height and diameter relative growth rates and percent visible foliar injury for 30 open pollinated loblolly pine families. The relative height growth rates contained a significant family by ozone interaction. Relative diameter growth rates had a significant family variation. There were no significant family effects observed for percent visible foliar injury. The change in relative height growth rate additive genetic variance and narrow sense heritability over increased ozone dosage indicated the presence of genetic control. Relative diameter growth rate additive genetic variance and heritability remained constant across increased ozone dosage. Thus, there were no indications of genetic control over the response of diameter relative growth rate to ozone. The lack of significant family variation in percent visible foliar injury indicated the lack of observable genetic control over this variable.

Keywords: Pinus taeda L., narrow sense heritability, phenotypic variation, dose response.

INTRODUCTION

Over the past decade an extensive research effort to determine the environmental impacts of pollution was sponsored by the United States government. Concerns over the effects of pollution from anthropogenic sources on forest ecosystems was addressed by the Forest Response Program (FRP). Long-term trends of ambient ozone in the southeastern United States suggested that ozone concentrations during the growing season often occur at levels sufficient enough to cause injury to plants (Pinkerton and Lefond 1987). A 1985 U. S. Forest Service report indicated that pines in the Georgia and South Carolina Piedmont region may have been in a growth decline. One of several possible causal agents mentioned in that report was ozone (Sheffeild et al. 1985). Ozone differs from most air pollutants in that it is a regionwide pollutant and not usually associated directly with a particular point source (Pinkerton and Lefond 1987). This fact led to including of ozone, with acid rain, in government sponsered studies involving southern pines.

[1/] Senior Scientist, Chemical Conversion Division, Solar Energy Research Institute, Golden, Colorado. The reported work was performed while the author was at Texas A&M University.

The detrimental effect of ozone on loblolly pine physiology and above grown growth has been established (Pye 1988, Reich 1987). Ozone enters the pine foliage through the stomates (Tingy and Hogsett 1985, Olsyzk and Tingy 1982). In the mesophyll layer inside the foliage ozone oxidizes cellular membranes (Heath 1980). The injury to the interior portions of the foliage can cause a reduction in net photosynthetic rates and/or an increase in respiration (Sasek and Richardson 1989, Hanson et al. 1988, Reich 1987). With less carbon inputs loblolly pine seedlings have been reported to change normal carbohydrate allocation patterns. Several studies reported that carbohydrates accumulate in the above ground portion of the seedling. Thus, the root to shoot ratios can change significantly due to ozone exposure (Wiselogel et al. 1990, Shafer and Heagle 1989, Pye 1988). A change in the root to shoot ration may predispose the seedling to drought or nutrient stress.

Several studies in Europe have reported the effect of genetic diversity on how forest trees respond to air pollution (Bergmann and Scholz 1987, Geburke et al. 1987). These studies employed isozymes to describe the genetic variation in air pollution resistance and susceptible tree populations. However, response to air pollution was characterized as visible foliar injury and not changes in physiological processes or reduction in growth. Studies with loblolly pine show a low correlation between visible foliar injury and growth reduction (Wiselogel et al. 1991, Adams et al. 1988, Pye 1988). Several reports on loblolly pine response to ozone have indicated the existence of genetic control (Wiselogel et al. 1991, Shafer and Heagle 1989, Adams et al. 1988). Shafer and Heagle (1989) reported a family by ozone interactions for loblolly pine seedling growth variables after 3 years of ozone treatments. Adams et al. (1988) observed similar results after one season of fumigation. The observed significant family by ozone interaction indicated that families perform differently as ozone concentrations increased. This trend is indicative expression of additive genetic control over the observed response.

A study by Wiselogel et al. (1991) observed family by ozone interactions for relative height growth rate and above ground biomass. This study was designed to screen the response of 30 commercially available open pollinated loblolly pine families to ozone induced stress. While not specifically designed for precise estimation of genetic variation the study does allow for its calculation. Thus, the study provided an opportunity to observe changes in genetic variation over increasing ozone concentrations.

METHODS

The study used 22-week-old seedlings from 30 open pollinated loblolly pine families. Prior to ozone treatments the seedlings had been grown in a charcoal-filtered greenhouse. Square wave dispensing of ozone in fumigation chambers occurred for 8 hours a day, 4 consecutive days a week, for 9 weeks. Ozone treatments of charcoal-filtered or > .01 ppm, .16 ppm, and .32 ppm were applied during the study. The ozone treatments resulted in ozone dosage exposures of — 1, 46, and 92 ppm hours-'. The study ozone dosages are comparable to ambient levels observed for the southeastern United States (Pinkerton and Lefond 1987). While the ozone exposures were of an artificial acute nature rather than a more natural chronic, there is evidence that both types of exposures have similar adverse effects on tree growth (Pye 1988, Reich 1987).

Due to the number of available fumigation chambers the experiment was design as a nested factorial with fumigation chamber effects confound in ozone treatments. To reduce the impact of confounded chamber effects on ozone treatments, seedlings and their ozone treatments were rotated to each chamber. Thus, each treatment was applied in every chamber an equal length of time. There were four replications within each ozone treatment. The replications were designed to block out position effects within the chambers. For a more detailed description of the study methodology see Wiselogel et al. (1991).

An analysis of variance (ANOVA) using PROC ANOVA (SAS 1982) was performed to determine ozone and family effects on monitored variables. Based on the results, relative height and diameter growth rate, and percent visible foliar injury were selected for genetic analysis. All sources of variation were considered random. Since the number of seedlings per family was small, the data was studentized to keep the narrow sense individual heritabilities below 1. Estimated mean squares were used to calculate phenotypic, genetic, and environmental variances for the variables of interest (SAS 1982). The open pollinated families were considered half-sib families to facilitate the calculation of heritabilities (Zobel and Talbert 1984).

Percent visible foliar injury (PVFI) was assessed on each seedling at the end of the study. PVFI was based on the proportion of the total foliar area which was chlorotic or necrotic. The percentage data was transformed with arcsin transformation as recommended by Snedecor and Cochran (1967) for binomial proportions. Relative growth rate for diameter and height was calculated as the difference between the natural log of the variable at the end and beginning of the study divided by the number of weeks in the study (Kramer and Kozlowski 1979).

RESULTS AND DISCUSSION

PVFI significantly increased with increased ozone dosage (Table 1). Chlorotic mottling and tip-burn was observed in the .32 ppm ozone treatment after 3 weeks and in the .16 ppm ozone treatment after 6 weeks.

Table 1. The probability of obtaining a greater f-test for percent visible foliar injury, relative diameter growth rate, and relative height growth rate of loblolly pine seedlings exposed to ---1, 46, and 92 ppm hours-^{1} ozone over 9 weeks.

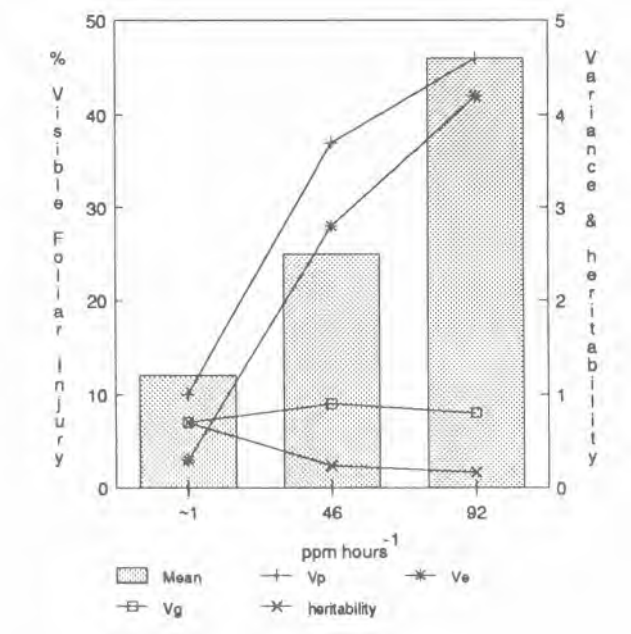
Source of Variation	Percent Visible Foliar Injury	Relative Diameter Growth Rate	Relative Height Growth Rate
Ozone	0.0153	0.0787	0.0012
Family	0.1535	0.0001	0.0001
Family x Ozone	0.8788	0.3264	0.0064

The visible injury for seedlings in the — 1 ppm hours' ozone treatment consisted of necrosis of primary needles and foliage injured during chamber rotations. At 31 weeks of age, mature secondary foliage was dominant in all seedlings and the juvenile primary foliage had or was senescent. Seedlings exposed to 46 ppm hours' of ozone exhibited a combination of chlorosis and tip-burn with only a few seedlings having just one or the other. All seedlings exposed to 92 ppm hours' of ozone had both chlorosis and tip-burn.

There were no significant family or family by ozone variation observed for PVFI. This indicated that PVFI is a poor variable for assessing genetic effects on loblolly pine seedling response to ozone. All open pollinated family relative performance was the same for each ozone treatment.

A linear increase in PVFI occurred with increased ozone dosage (Figure 1). As PVFI increased the proportion of genetic and environmental variation in the phenotypic variation changed. At the low ozone treatment, narrow sense individual heritability (h^2) was observed to be 0.7. The high h^2 could have resulted from genetic control over the senescence of primary foliage. As ozone dosage increased so did phenotypic and environmental variation. The constant level of genetic variation resulted in a rapid decrease in h^2 of PVFI.

Figure 1. The mean response of percent visible foliar injury, phenotypic variation (Vp), additive genetic variation (Vg), environmental variation (Ve), and narrow sense individual heritabilities to ozone.

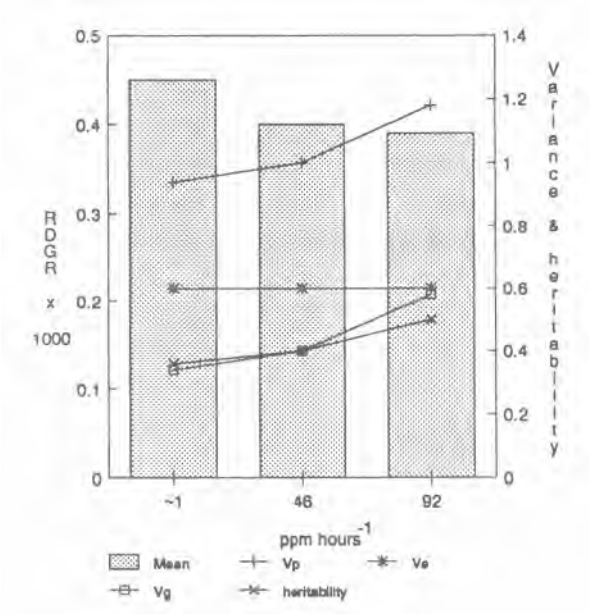


Relative diameter growth rate (RDGR) was not as responsive to ozone treatments as PVFI. The results of the ANOVA suggested that the majority of variation observed for RDGR was located among families (Table 1). These family differences remained constant across increased ozone dosage as indicated by the non-significant family by ozone interaction.

The reduction of RDGR by ozone was not linear in respect to dosage (Figure 2). There

was essentially no difference between the response of loblolly pine seedlings to 46 and 92 ppm hours-[1] ozone. With the increased ozone dosage, the phenotypic and genetic variation for RDGR increased by 20% while the environmental variation remained constant. This response resulted in a slightly increased h^2. The change in h^2 did not result in a change of family performance, thus, there is no indication of genetic control over RDGR response to ozone. The families with the highest RDGR under pristine conditions had the highest growth rate under high ozone conditions.

Figure 2. The mean response of relative diameter growth rate, phenotypic variation (Vp), additive genetic variation (Vg), environmental variation (Ve), and narrow sense individual heritabilities to ozone.



All sources of variation were significant for relative height growth rate (RHGR) (Table 1). As ozone dosage increased open pollinated families responded differently. The resultant significant family by ozone interaction indicated that genetic control existed over the response of RHGR to ozone. RHGR decreased with increased ozone dosage (Figure 3). The phenotypic variation remained constant as ozone dosage increased, however, genetic variation increased and environmental variation decreased. As a result, h^2 increased with ozone dosage. The change in h^2 supported the existence of genetic control over RHGR response to ozone as implied by the family by ozone interaction observed in the ANOVA.

Of the 30 open pollinated families used in the study, 22 families had a non-significant decrease in RHGR with increased ozone dosage (Figure 4). Seven families had a significant decrease in RHGR with increased ozone dosage, and 1 family increased RHGR at 92 ppm hours-' ozone. Family 8-80 was among the slowest growing families for — 1 and 46 ppm hours' ozone and intermediate in RHGR for 92 ppm hours' ozone. The significant change in performance for 8 of the 30 open pollinated families indicated that genetically endowed responce to ozone existed for the RHGR. The degree to which ozone effects tree height at time of evaluation for progeny test will determine if commercial populations in areas with high ambient

ozone are selected for ozone resistance.

Figure 3. The mean response of relative height growth rate, phenotypic variation (Vp), additive genetic variation (Vg), environmental variation (Ve), and individual narrow sense heritabilities to ozone.

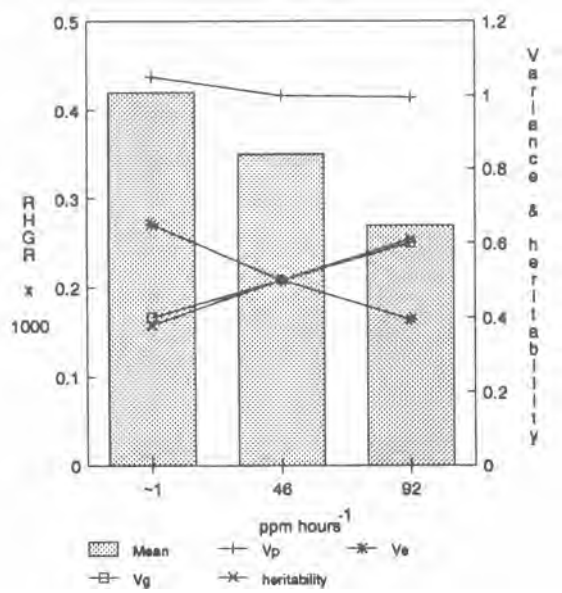
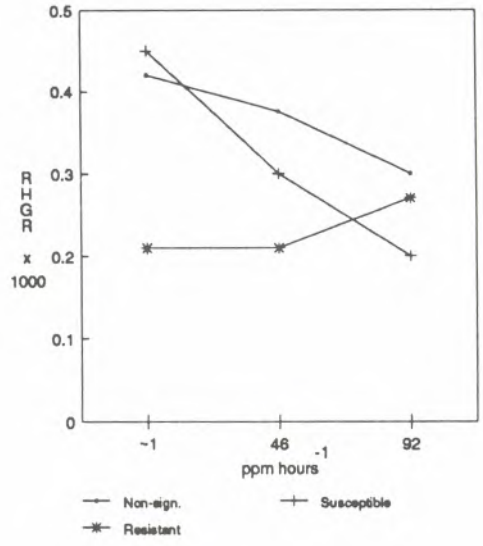


Figure 4. The relative height growth response of the 22 non-significantly effected families, 8 susceptible families, and the resistant family to ozone.



CONCLUSIONS

The use of percent visible foliar injury as a measure of loblolly pine response to ozone is tenuous. This study provided no evidence of genetic control over the visible foliar injury response to ozone. Relative diameter growth rate was the least sensitive of the response variables to ozone. The relative rankings of open pollinated family performance were not affected by increased ozone dosage. Relative height growth rate provided evidence of genetic control over the seedlings response to ozone dosage. If this fact is true, then it could be possible that loblolly pine families may have been selected or rogued because of their genetic response to ozone.

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