Forest Science, Vol. 37, No. 6. pp. 1538–1549

Seedling Responses of Five Species of Western Conifers to Simulated Ambient Sulfur Dioxide Exposures

THEODOR D. LEININGER
PAUL R. MILLER
SUSAN L. SCHILLING
PAUL H. DUNN

ABSTRACT. Seedlings of ponderosa pine, Douglas-fir, white fir, Engelmann spruce, and subalpine fir were exposed continuously to charcoal-filtered (CF) air or one of three levels of a simulated ambient exposure typical of SO_2 pollution near smelters in the western United States. Seedlings were exposed during winter-spring experiments for 60 days to hourly means of 17, 38, and 54 ppb in 1988 and 35, 57, and 99 ppb in 1989. Sensitivities of species to SO_2 were determined from height growth, diameter growth, root, stem, and needle weights, and from foliar injury.

Ponderosa pine in all SO_2 treatments in 1989 had decreased diameter growth and decreased needle weights compared with those in CF air. In 1989, average diameter growth of Douglas-fir in ail SO_2 treatments was less than those in CF air. Diameter growth and needle weights of ponderosa pine were correlated in all SO_2 treatments and CF air. Diameter growth and needle weights of Douglas-fir were correlated in all SO_2 treatments. Tip necrosis of needles occurred on a larger proportion of seedlings of all species in high SO_2 than on those in CF air. Ponderosa pine and Douglas-fir were about equally sensitive to SO_2 and both were more sensitive than white fir. White fir was more sensitive to SO_2 than Engelmann spruce and subalpine fir which were equally unresponsive to SO_2. FOR. SCI. 37(6):1538–1549.

ADDITIONAL KEY WORDS. Ponderosa pine, Douglas-fir, white fir, Engelmann spruce, subalpine fir.

SULFUR DIOXIDE (SO_2) AS A POLLUTANT can damage forest tree species, especially in areas downwind of major anthropogenic SO_2 sources (Smith 1990). Studies reviewed by Kozlowski and Constantinidou (1986) indicated that SO_2 can reduce needle growth, height growth, diameter growth, and biomass of conifers. Other studies reviewed by the same authors described damage to mesophyll parenchyma, epidermis, and vascular tissues of conifer needles leading to visible symptoms of chlorosis, necrosis, and premature abscission. Foliar injury was used to rank species sensitivity to SO_2 in studies reviewed by Davis and Wilhour (1976).

This study used measurements of foliar injury, height, stem diameter, and biomass to determine relative sensitivities to SO_2 of ponderosa pine (*Pinus ponderosa* ex P. Laws. & C. Laws.), Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), white fir (*Abies concolor* [Gord. & Glend.] Lindl. ex Hildebr.), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), and subalpine fir (*Abies*

Reprinted from *Forest* Science, Vol. 37, No. 6, December 1991

lasiocarpa [Hook.] Nutt.). Exposure regimes simulated frequencies, durations, and concentrations of worst-case scenarios for SO, originating from smelters in the western United States. Species were selected on the basis of their geographic extent in the western United States, and their importance to the economy of the region.

EXPERIMENTAL METHODS

PLANT CULTURE

Two-year-old, bareroot white fir seedlings and one-year-old, container-grown ponderosa pine seedlings were obtained from the California Department of Forestry nursery at Ben Lomond in 1987 and 1988. White firs originated in California seed zone 531 (1,372 m, western Sierras). Ponderosa pines were from California seed zone 522 (610 m, western Sierras). Two-year-old, bareroot Engelmann spruce seedlings were obtained from the USDA Forest Service Lucky Peak Nursery, Boise, ID in 1986 for exposures in 1988, and again in 1988 for exposures in 1989. The source of Engehnann spruce seed was Warm Lake, ID. One-year-old, container-grown Douglas-fir seedlings were obtained from Cavenham Forest Industries, Inc., NW Timber Nursery, Aurora, OR, in 1987, and from Rex Timber, Inc., Cottage Grove, OR, in 1988. Douglas-fir was obtained from Oregon seed zone 471 (610 m, western Cascades). Two-year-old subalpine fir seedlings in containers were obtained from Plants of the Wild, Tekoa, WA in 1986 for exposure in 1988, and again in 1988 for experiments in 1989. Subalpine fir seed source was south of Lewiston, ID (1,372 m).

In April 1986, 1987, and 1988, seedlings were transplanted to Dee-cells (6.4 cm x 25.4 cm, Stuewe and Sons, Corvallis, OR) in Pro-Mix B:perlite (1:1 v/v). Soil moisture optimal for plant growth was maintained by adding tap water through a drip irrigation system (Chapin Watermatics Inc., Watertown, NY). A solution of liquid nutrients (North Carolina State University Phytotron Nutrient Mix) was applied once every 2 to 3 weeks from March through October 1987 and once every 1 to 2 weeks from March through October 1988. Plants were not fertilized between October and March in either year. Prior to fumigation, plants were kept in a greenhouse in which the air was filtered through charcoal and cooled by evaporation. The greenhouse was located at 1,387 m in the San Jacinto Mountains 22 km southeast of Idyllwild, CA (33°37′N, 116°37′W).

SO, EXPOSURE SYSTEM

Plants were exposed to SO, in modified open-top chambers (Hogsett et al. 1985) under ambient environmental conditions from March 4 to May 5, 1988, and from February 9 to April 9, 1989. Chambers were located in Riverside, CA (33°57′N, 117°20′W). All chambers were supplied with charcoal-filtered (CF) air. Sulfur dioxide was dispensed from a heated cylinder of anhydrous SO, and diluted with dry air from a heatless air dryer (General Cable Co., Westminster, CO). Sulfur dioxide for each treatment was introduced into the incoming stream of CF air via a mass flow controller (Edwards High Vacuum International, Wilmington, MA) regulated by a control and data acquisition system (Hogsett et al. 1985). Concentrations of SO, in chambers were measured with a Dasibi model 4108 fluorescence SO, analyzer (Dasibi Environmental Corp., Glendale, CA).

The data acquisition system recorded hourly averages of air temperature, soil mix temperature, and photosynthetically active radiation (PAR) in one chamber. A hygrothermograph in the same chamber recorded relative humidity (RH). Hourly averages of air temperature, PAR, and RH outside the chambers were recorded by the data acquisition system. In 1989, a hygrothermograph recorded temperatures and RH to which plants were exposed in the greenhouse before being harvested. Relative humidity and PAR during experiments were similar in both years. The 1988 experiment was begun a month later in the year than the 1989 experiment. As a result, chamber air temperatures and soil mix temperatures reached peaks that exceeded those for optimal plant growth several times during the last half of the 1988 exposure. High temperatures resulted in severe wilting and premature needle loss which led to the decision not to harvest seedlings for biomass measurements in 1988.

EXPOSURE REGIME

Plants were exposed to SO, according to a regime that simulated frequencies, durations, and concentrations of SO, events recorded near metal smelters in the western United States (Hogsett et al. 1989, Lefohn et al. 1986). The base profile represented the worst-case, high treatment with an hourly average concentration of 66 ppb SO, over 60 days. Hourly SO, concentrations in the base profile ranged from 0 to 2500 ppb (Figure 1). A medium treatment profile was made by reducing hourly concentrations and the frequency of SO, events of the base profile to yield an hourly average concentration of 44 ppb SO,. A low treatment profile was made by reducing hourly concentrations and the frequency of SO, events of the base profile to yield an hourly average concentration of 22 ppb SO_2. Hourly average SO, concentrations in 1988 were 54, 38, and 17 ppb for high, medium, and low treatments, respectively; in 1989 they were 99, 57, and 35 ppb for high, medium, and low treatments, respectively. Despite deviations from request concentrations and differences between the 2 years, percent differences between high, medium, and low treatments were maintained. Plants were treated during winter and spring, because SO, concentrations in the air quality data record were highest then.

EXPERIMENTAL DESIGN AND BIOLOGICAL MEASUREMENTS

In 1988, 48 seedlings of each species were placed in each of eight chambers; two chambers for each of three treatment levels, and two control chambers. Heights and diameters of stems were measured before and after the fumigation. Stem heights were measured from the cotyledon scar to the tip of the apical bud. An ink line marked a level 2 mm below the cotyledon scar at which diameters were measured. The mean of three diameter measurements was recorded for each seedling.

In 1989, 20 previously unexposed seedlings of each species were placed in each chamber. Heights and diameters of stems were measured before and after the fumigation. After the fumigation, foliar injury of each seedling was estimated by eye in increments of 10% of total crown area. Injury symptoms included in the

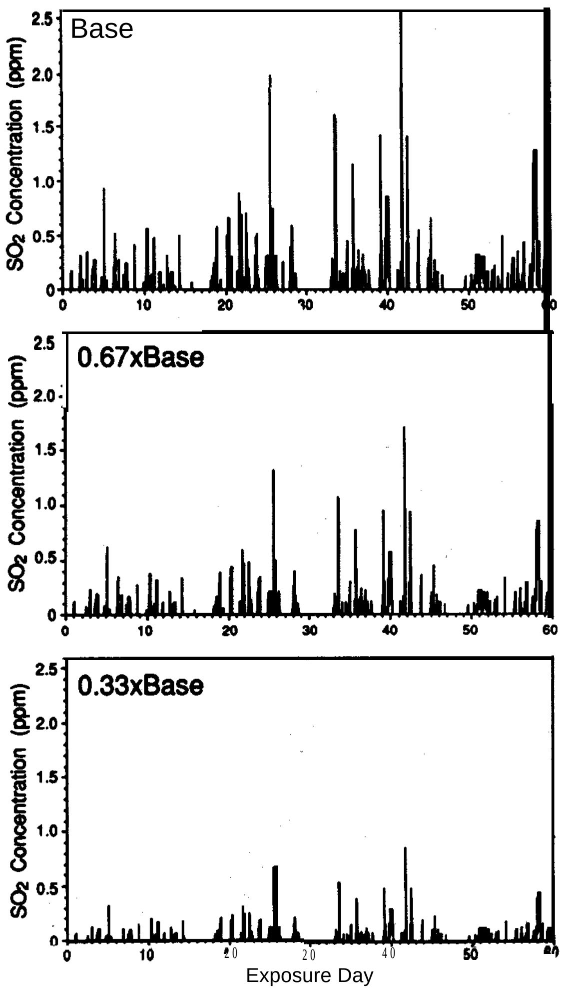

FIGURE 1. Simulated exposure profiles for sulfur dioxide.

estimate were tip necrosis, necrotic banding, and premature needle abscission (abscission of current-year or l-year-old needles). A normal approximation to the binomial distribution was used to evaluate differences in the proportions of trees in each treatment that showed foliar injury. Seedlings were maintained in an air-conditioned greenhouse until early August 1989 when they were harvested and separated into roots, stems, and foliage. Root, stem, and foliar tissue was dried in an oven for 72 hr at 70°C before being weighed separately on an electronic scale.

Height and diameter growth data from the five species were analyzed separately and were compared between treatments by one-way analysis of variance (ANOVA) using the mean response of the chambers as the analysis variable. Separation of means was tested when the overall p-value of the ANOVA was ≤ 0.10. Linear contrasts were used to compare the response of trees in CF air with the average response of trees in all SO_2 treatments.

The model used to test biomass variables was nested (chambers within treatments) and included initial height as a covariate. The covariate was significant for all species. Treatments were fixed and chambers were random. Sample size was reduced to 15 seedlings per species per chamber through a combination of mortality which occurred uniformly in all chambers, and random selection. Separation of means was tested using linear contrasts when the overall p-value of the ANOVA was ≤0.10. Linear contrasts were used to compare average weight variables of seedlings exposed to all SO, treatments with those exposed to CF air.

RESULTS

HEIGHT AND DIAMETER GROWTH

Effects of SO_2 on height growth after exposures in 1988 were significant for white fir (*P* = 0.03) and Engelmann spruce (*P* = 0.01) but not for ponderosa pine, Douglas-fir, or subalpine fir (Figure 2). Height growth of white fir exposed to medium doses of SO, was 71% greater than that of white fir in CF air. Height growth of white fir in all SO, treatments averaged 39% more (*P* = 0.03) than that of white fir exposed to CF air. Engelmann spruce in medium and high treatments had 111% and 99% more height growth, respectively, than spruce in CF air.

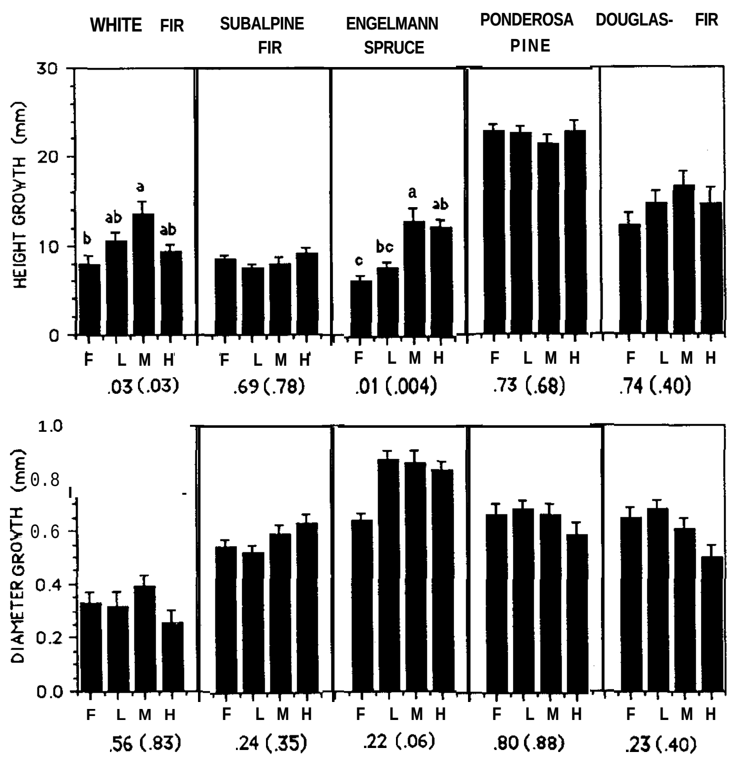

FIGURE 2. Height and diameter growth of five western conifer species exposed to SO, and charcoal-filtered air in 1988. F = charcoal-filtered air, H = base treatment, M = base*0.67, and L = base*0.33. Standard errors about the means are shown. Different lowercase letters indicate means separations. P-values of ANOVAs are beneath data plots for each species. P-values of linear contrasts comparing average height and diameter growth of seedlings exposed to all SO, treatments with those of seedlings in CF air are in parentheses.

Height growth of Engehnann spruce in all SO_2 treatments averaged 78% more (P = 0.004) than that of spruce exposed to CF air. Effects of SO_2 on height growth following the 1989 experiment were not significant for any of the species (Figure 3).

Effects of SO_2 on diameter growth of all species treated in 1988 were not significant (Figure 2). Linear contrasts indicated that average diameter growth of Engehnann spruce in all SO_2 treatments in 1988 was 33% greater (P = 0.06) than that of Engehnann spruce exposed to CF air. In 1989, diameter growth of ponderosa pine averaged 31% less (P = 0.004) in SO_2 treatments than in CF air (Figure 3). Diameter growth of Douglas-fir exposed to all SO_2 treatments averaged 25% less (P = 0.07) than that of Douglas-fir in CF air. Exposure to SO_2 did not significantly affect diameter growth of Engehnann spruce, subalpine fir, or white fir in 1989.

Average height and diameter growth for all treatments for all species in 1988 were about half of those in 1989. Seedlings obtained for the 1988 exposures were generally smaller than those obtained for 1989. Severe wilting and premature needle abscission brought on by high temperatures in 1988 may have suppressed height and diameter growth.

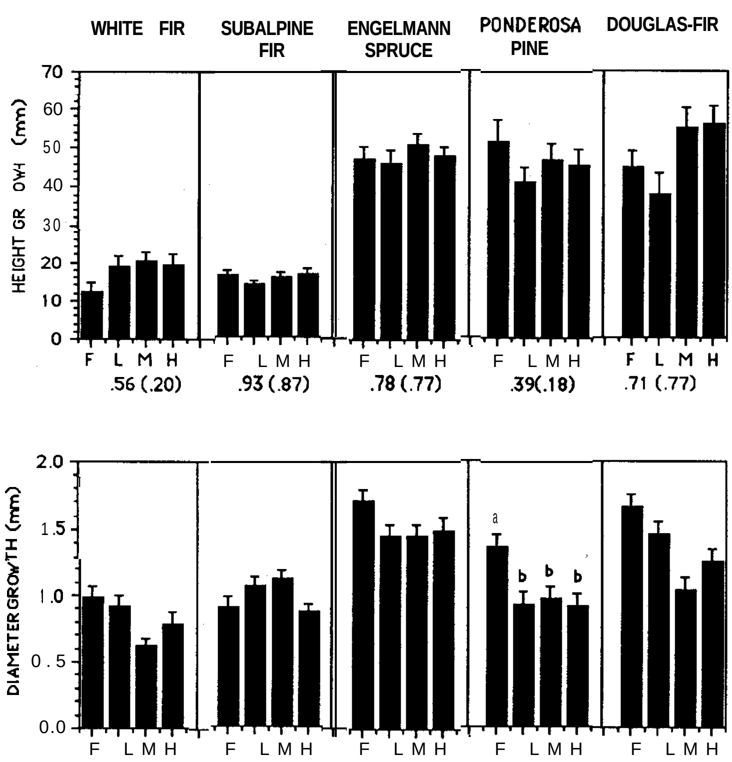

FIGURE 3. Height and diameter growth of five western conifer species exposed to SO_2 and charcoal-filtered air in 1989. F = charcoal-filtered air, H = base treatment, M = base*0.67, and L = base*0.33. Standard errors about the means are shown. Different lowercase letters indicate means separations. P-values of ANOVAs are beneath data plots for each species. P-values of linear contrasts comparing average height and diameter growth of seedlings exposed to all SO_2 treatments with those of seedlings in CF air are in parentheses.

The values for dry weights of ponderosa pine foliage from the high, medium, and low SO_2 exposures in 1989 were less than (*P* = 0.10) those in CF air (Figure 4), and the average weight of ponderosa pine foliage exposed to all SO_2 treatments was 19% less than (*P* = 0.10) that in CF air. Average root and stem weights of ponderosa pine exposed to all SO, treatments were, respectively, 18% and 14% less than those exposed to CF air, although differences were not statistically

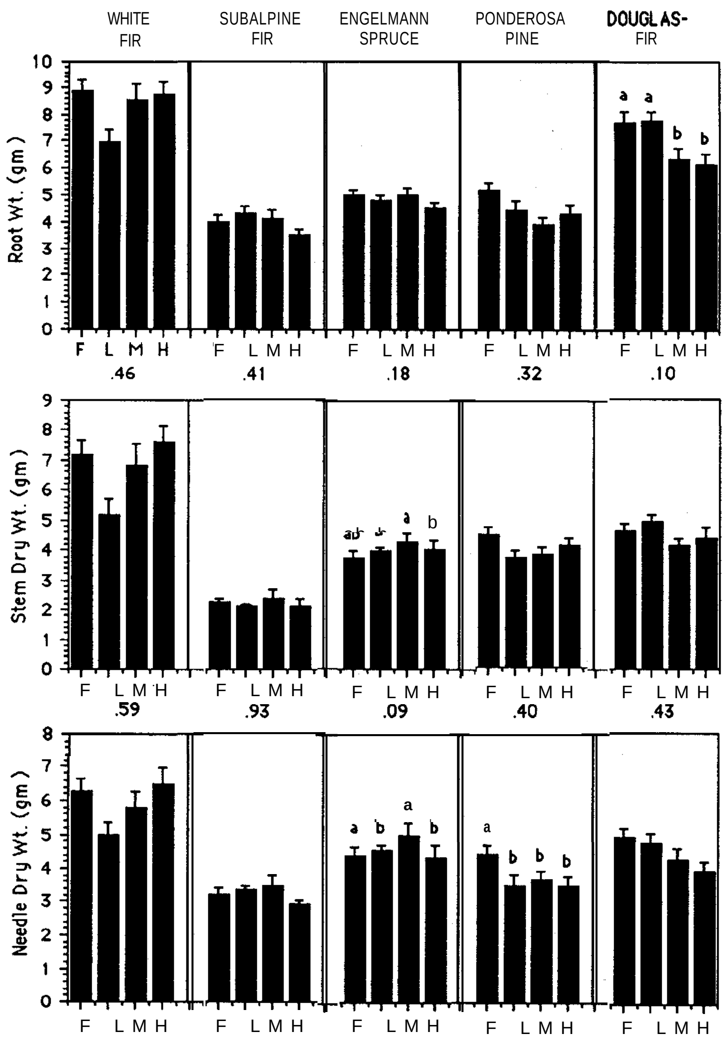

FIGURE 4. Average dry weights of roots, stems, and foliage of five species of western conifers exposed to SO, in 1989. Means are not adjusted by the covariate initial height. Standard errors about the means are shown. F = charcoal-filtered air, H = base treatment, M = base*0.67, and L = base*0.33. P-values for treatment effects are beneath data plots for each species. Different lowercase letters indicate means separations. Significant linear contrasts (*P* ⩽ 0.10) comparing average weight variables of seedlings exposed to ail SO, treatments with those of seedlings in CF air are denoted by**.

significant. Roots of Douglas-fir exposed to medium and high SO_2 doses weighed an average of 18% less than (P = 0.10) those exposed to low SO_2 doses and CF air (Figure 4). Although the difference was not statistically significant, the average weight of Douglas-fir foliage exposed to high and medium doses of SO_2 was 15% less than that exposed to low doses of SO_2 and CF air. Analysis of covariance (ANCOVA) tests were significant for stem (P = 0.09) and foliage (P = 0.02) weights of Engelmann spruce, but means separations showed no clear relationship between SO_2 dose and these variables (Figure 4). ANCOVA tests were not significant for white fir or subalpine fir. There was an unusual trend of increasing root, stem, and needle weights with increasing SO_2 dose for white fir.

Foliage weights of ponderosa pine exposed to all treatments and foliage weights of Douglas-fir exposed to low, medium, and high doses of SO_2 were significantly correlated with diameter growth (Table 1). The remaining significant correlations of weight variables with diameter or height growth of ponderosa pine, Douglas-fir,

TABLE 1.

Correlation coefficients relating stem diameter growth or height growth to dry weights of roots, stems, or needles of seedlings exposed to SO_2 treatments and charcoal-filtered air in 1989.

Species and treatment	Correlation between diameter growth and dry weights of			Correlation between height growth and dry weights of		
	Roots	Stems	Needles	Roots	Stems	Needles
Ponderosa pine						
Filtered-air	0.41	0.58*	0.61*	0.30	0.20	0.37
Low	0.36	0.60*	0.75***	0.64**	0.58*	0.41
Medium	0.45	0.43	0.69***	0.27	0.26	0.32
High	0.41	0.46	0.72***	0.48	0.53	0.42
Douglas-fir						
Filtered-air	0.18	0.42	0.50	-0.07	0.22	0
LOW	0.62**	0.47	0.67***	0.04	0.20	0.22
Medium	0.31	0.58*	0.68***	0.01	0.17	0.15
High	0.65**	0.57*	0.70***	0.30	0.47	0.46
White fir						
Filtered-air	0.16	0.32	0.17	-0.40	-0.43	-0.45
Low	0	0	0.06	-0.39	-0.41	-0.30
Medium	-0.06	-0.06	0.08	-0.20	-0.28	-0.11
High	0.05	0.20	0.21	0.01	0.10	0.07
Engelmann spruce						
Filtered-air	0.10	0.20	0.02	0.14	0.24	0.35
Low	0.05	0.27	-0.02	-0.17	0	0.14
Medium	-0.10	-0.18	-0.21	-0.06	0.05	0
High	0.53+	0.44	0.31	-0.08	0	0.09
Subalpine fir						
Filtered-air	0.69**	0.30	0.74***	0.26	-0.01	0.35
LOW	0.44	0.14	0.29	0.09	-0.25	0.02
Medium	0.22	0.05	0.12	0.43	0.28	0.27
High	0.42	0.41	0.47	0.23	0.27	0.35

Bonferonni adjusted probabilities of significant correlation coefficients; *** = $P \leqslant 0.002$, ** = $\leqslant 0.01$, * = $P \leqslant 0.05$, and + = $P \leqslant 0.10$.

Engelmann spruce, and subalpine fir occurred without any apparent pattern. There were no significant correlations of any variables for white fir.

Effects of exposure on the ratios of root weights to weights of the following: stems, first-year foliage, second-year foliage, first-year plus second-year foliage, stems plus first- and second-year foliage, stems plus first-year foliage, and stems plus second-year foliage were tested by ANOVA. There were no statistically significant differences among treatments (data not shown).

FOLJAR INJURY

The most common needle injury symptom was tip necrosis. A greater proportion of trees of all species exposed to high doses of SO, had needle tip necrosis compared with those in CF air (Table 2). A greater proportion of ponderosa pine, Douglas-fir, and white fir exposed to medium doses of SO, had needle tip necrosis compared with those in low doses of SO, and CF air. Average percentages of

TABLE 2.

Tip necrosis and necrotic banding on foliage of five species of western conifers treated with SO, and charcoal-filtered air in 1989.

Species and treatment	Total number of trees per treatment	Number of trees with needle tip necrosis	Average % crown with needle tip necrosis	Number of trees with necrotic banding	Average % crown with necrotic banding
Ponderosa pine					
Filtered-air	37	3 c	21	0 b	0
Low	39	5 c	20	0 b	0
Medium	40	12 b	26	3 a	7
High	38	23 a	36	6 a	14
Douglas-fir					
Filtered-air	37	4 c	20	0 b	0
Low	40	4 c	38	0 b	0
Medium	39	16 b	27	1 b	10
High	39	26 a	37	11 a	9
White fir					
Filtered-air	38	2 c	8	0 b	0
Low	38	1 c	20	0 b	0
Medium	40	13 b	16	1 b	1
High	39	22 a	44	4 a	10
Engehnann spruce					
Filtered-air	38	1 b	90	0	0
Low	36	1 b	10	1	30
Medium	40	2 b	22	0	0
High	39	15 a	36		10
Subalpine fir					
Filtered-air	38	16 bd	25	1	30
LOW	40	10 c	16	0	0
Medium	40	21 ad	22		5
High	40	27 a	25	2	8

Different lowercase letters indicate differences ($P \leqslant 0.05$) in the proportion of trees among treatments within a species affected by needle tip necrosis and necrotic banding based on an approximation to the normal distribution.

crowns damaged by tip necrosis on affected ponderosa pine and white fir increased as SO_2 dose increased. A greater proportion of ponderosa pine in high and medium SO_2 treatments had necrotic banding compared with those in low SO_2 treatments and CF air. The average percentage of crowns damaged by necrotic banding on affected ponderosa pines in the high SO_2 treatment was twice that of those in the medium SO_2 treatment. The proportion of Douglas-fir and white fir with necrotic banding was greater in high doses of SO_2 than in low and medium doses of SO_2 and CF air. Twenty seedlings of each species exposed to the high SO_2 treatment and CF air were assessed for premature needle loss at the end of the 1989 experiment. A greater proportion ($P \leq 0.05$) of Douglas-fir, white fir, and Engelmann spruce exposed to high doses of SO_2 lost needles prematurely compared with those exposed to CF air (data not shown).

DISCUSSION

The most consistent response of all species was a significant increase in needle tip necrosis associated with increasing SO_2 dose. Necrotic banding occurred more often on ponderosa pine, Douglas-fir, and white fir exposed to high doses of SO_2 than on those in CF air. Needle tip necrosis and necrotic banding are common foliar symptoms of conifers exposed to SO_2 (Skelly et al. 1987). Foliar injury symptoms were more common on seedlings of all species in 1989 than were effects to stem dimensions and biomass. This was probably due to the short duration of the experiment and the fact that the exposure was begun a few weeks prior to bud break. Seedlings of all species were dormant when the fumigation began. Engelmann spruce and subalpine fir "broke bud" after 13 days of exposure in 1989. Growth of ponderosa pine, Douglas-fir, and white fir had begun by the end of the first half of the 1989 exposure. Thus, the observed decreases in diameter growth and needle weights of ponderosa pine, and decreases in diameter growth and root weights of Douglas-fir in 1989 were most probably effects of SO_2 exposure on expanding current-year foliage.

Diameter growth, foliage weights, and foliar injury of ponderosa pine and Douglas-fir in 1989 showed more negative effects from SO_2 than white fir, Engelmann spruce, and subalpine fir. For ponderosa pine and Douglas-fir in 1989, there was a link between SO_2 dose, reduced diameter growth, and less total foliage weight. Indeed the average total foliage weight of ponderosa pine seedlings exposed to all SO_2 treatments was less than that of those in CF air. Exposing ponderosa pine to hourly mean concentrations of 57 and 99 ppb SO_2 had no greater effect in decreasing diameter growth and foliage weights than did an hourly mean of 35 ppb. This response of ponderosa pine suggests a threshold dose at which damage from SO_2 occurs, a concept advanced by O'Gara (1922). However, all three treatment doses of SO_2 in our study were administered over 60 days, and we did not expose any seedlings to high concentrations of SO_2 over short time periods (e.g., several hours).

The statistically significant differences among treatments from the 1988 exposure (Figure 2) were not substantiated by data from the 1989 exposure. It is unclear whether the instances of increased height and diameter growth in 1988, in seedlings exposed to SO_2 compared to those in CF air, are effects of treatments or aberrations affected by heat stress. In any case, a stress-induced stimulation of shoot growth may not benefit seedlings but may indicate a shift in carbon allocation, perhaps to repair or replace damaged tissue.

Based on our results, ponderosa pine and Douglas-fir were about equally sensitive to SO_2, and both were more sensitive than white fir. White fir was more sensitive to SO, than Engelmann spruce and subalpine fir, which were about equally unresponsive to SO,. Previous observations of foliar injury on mature trees resulted in the following rankings of species in order of decreasing sensitivity to SO,; Douglas-fir, ponderosa pine, Engelmann spruce, and white fir (Katz et al. 1939); and subalpine fir, Douglas-fir, Engelmann spruce, and ponderosa pine (Scheffer and Hedgecock 1955). The exposure which most closely resembled that of our study was the natural field exposure reported by Scheffer and Hedgecock (1955). The difference in tree ages may explain why their results differed from ours.

Previous experiments with seedlings produced the following rankings of species from most to least sensitive: Douglas-fir, subalpine fir, ponderosa pine, and white fir (Hi et al. 1974); and from intermediate to tolerant: ponderosa pine, Douglas-fir, Engelmann spruce, and white fir (Davis and Wiiour 1976, Davis and Gerhold 1976). Results of "square-wave" fumigations reported by Hill et al. (1974) and Davis and Gerhold (1976) are difficult to compare with those of our simulated exposure profile. Ponderosa pine has been described as sensitive (Linzon 1972), "relatively susceptible" (Barrett and Benedict 1970), and "very susceptible" (Ranft and Dassler 1970) to SO,. Douglas-fir has been described as sensitive to SO, (Linzon 1972). These descriptions agree with our findings.

The purpose of using winter-spring exposures was to simulate actual conditions near point sources of SO,. In winter, cold night temperatures cause ground-based inversions to persist until late morning, allowing the buildup of SO,. The exposure profile used in our experiments supplied many of the highest concentrations when light was limited, a time when stomates are usually closed. Maclean et al. (1986) found that Douglas-fir and four species of pine did not accumulate sulfur and did not develop foliar injury when fumigated in winter with concentrations of SO_2 that would have produced injury in summer. Our results, indicating the sensitivity of ponderosa pine and Douglas-fir to SO,, are best applied in the context of winter-spring exposures near point sources of SO, in the western United States.

LITERATURE CITED

BARRETT, T.W., and H.M. BENEDICT. 1970. Sulfur dioxide. P. Cl-Cl7 *in* Recognition of air pollution injury to vegetation. A pictorial atlas, Jacobson, J.S., and A.C. Hill feds.). Air Pollut. Control Assoc., Pittsburgh, PA.

DAVIS, D.D., and H. GERHOLD. 1976. Selection of trees for tolerance to air pollutants. USDA For. Serv. Gen. Tech. Rep. NE-22, 61-66.

DAVIS, D.D., and R.G. WLHOUR. 1976. Susceptibility of woody plants to sulfur dioxide and photochemical oxidants. Corvallis Environ. Res. Lab., Office of Res. and Dev., U.S. Environmental Protection Agency, Corvallis, OR.

HILL, A.C., S. HLL, C. LAMB, and T.W. BARRETT. 1974. Sensitivity of native vegetation to SO, and to NO, combined. J. Air Pollut. Control Assoc. 24:153–157.

HOGSETT, W.E., D.T. TINGEY, and S.R. HOLMAN. 1985. A programmable control system for determination of the effects of pollutant exposure regimes on plant growth. Atmos. Environ. 19: 1135-1145.

HOGSETT, W.E., D.T. TINGEY, C. HENDRICKS, and D. Rosa. 1989. Sensitivity of Western conifers to SO_2 and seasonal interaction of acid fog and ozone. P. 469-491 *in* Effects of air pollution on Western forests, Olson, R.K., and A.S. Lefohn (eds.). Air and Waste Water Management Assoc., Pittsburgh, PA.

KATZ, M., G.A. LEDINGHAM, and A.W. MCCALLUM. 1939. Symptoms of injury on forests and crop plants. P. 51-103 *in* Effect of sulphur dioxide on vegetation. NRC No. 815. National Research Council of Canada, Ottawa.

KOZLOWSKI, T.T., and H.A. CONSTANTINIDOU. 1986. Responses of woody plants to environmental pollution. For. Abstr. 47:5–51.

LEFOHN, A.S., W.E. HOGSETT, and D.T. TINGEY. 1986. The development of sulfur dioxide and ozone exposure profiles that mimic ambient conditions in the rural southeastern United States. Atmos. Environ. 21:659–669.

LINZON, S.N. 1972. Effects of sulphur oxides on vegetation. For. Chron. 48:182–186.

MACLEAN, D.C., R.E. SCHNEIDER, and L.H. WEINSTEIN. 1986. Responses of five species of conifers to sulfur dioxide and hydrogen fluoride during winter dormancy. Environ. Exp. Bot. 26:291–296.

O'GARA, P.J. 1922. Sulfur dioxide and fume problems and their solutions. Ind. Eng. Chem. 14:744.

RANFT, H., and H.G. DASSLER. 1970. Smoke-hardiness test carried out on woods in an SO_2 chamber test. Flora 159:573–588.

SCHEFFER, T.C., and C.G. HEDGECOCK. 1955. Injury to northwestern forest trees by sulfur dioxide from smelters. USDA For. Serv. Tech. Bull. No. 1117. Washington, DC. 49 p.

SKELLY, J.M., ET AL. (eds.). 1987. Diagnosing injury to Eastern forest trees. Agricultural Information Services, The Pennsylvania State University and USDA Forest Service. 122 p.

SMITH, W.H. 1990. Air pollution and forests: Interactions between air contaminants and forest ecosystems. Ed. 2. Springer-Verlag, New York.

Manuscript received December 18, 1990

AUTHORS AND ACKNOWLEDGMENTS

Authors Leininger, Miier, and Schilling are with the USDA Forest Service, Pacific Southwest Forest and Range Experiment Station, 4955 Canyon Crest Drive, Riverside, CA 92507. Paul Dunn is with the USDA Forest Service, Forest Environment Research, South Building, 12th and Independence Ave. SW, Washington, DC 20250. We thank David Larson, Anthony Gomez, David Herring, Berdine Heckmann, and Thomas Ferguson for their technical assistance during the project. We thank Andrzej Bytnerowicz, Roberta Burzynski, Mark Fenn, Donald Maclean, David Randall, Patrick Temple, and John Skelly for reviewing the manuscript. Financial support was provided by the U.S. Environmental Protection Agency and USDA Forest Service under the auspices of the Western Conifers Research Cooperative, Forest Response Program. Mention of trade names or products is for information only and does not imply endorsement by the U.S. Department of Agriculture.