Air Pollution Effects on Giant Sequoia Ecosystems[1]

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Abstract: Giant sequoia [*Sequoiadendron giganteum* (Lindl.) Buchholz] groves are found entirely within the Sierra Nevada mixed-conifer type. Several of its companion tree species, mainly ponderosa pine *(Pinus ponderosa* Dougl. ex Laws.) and Jeffrey pine *(P. jeffreyi* Grev. & Balf.), show foliar injury after exposure to present levels of ozone in the southern Sierra Nevada. Observations at nine giant sequoia groves in Sequoia National Park from August 1983 through September 1986 showed that surviving seedlings in 1986 averaged 18 percent of the original number. These observations did not provide evidence of a causal relationship between ozone exposure and seedling mortality. Field fumigation studies with container-grown seedlings at Giant Forest during the summers of 1987 and 1988 tested morphological and physiological responses of seedlings exposed to charcoal-filtered air, I X, and 1.5X the ambient ozone concentration for the entire summer season. In both 1987 and 1988, very slight levels of visible ozone injury to cotyledonary and primary leaves were observed in fumigation chambers and at sites in natural groves at 1X ambient ozone concentrations; however, at 1.5X ambient in chambers the symptoms of foliar injury were extensive. The end-of-season harvests of seedlings exposed to 1.5X ambient ozone showed no significant reductions of root, shoot, or total plant weights in 1987 or 1988. Gas exchange measurements made during the 1988 experiment found that ozone exposure of seedlings and rooted cuttings to 1.5X ambient ozone over the duration of a growing season increased the light compensation point, lowered CO, exchange rate at light saturation, and increased dark respiration compared to controls. A 2-month branch-chamber fumigation of large giant sequoia saplings (120 years old) with charcoal- filtered air and ozone at IX, 2X, and 3X ambient ozone concentrations did not yield visible injury or any detectable changes in photosynthetic rates.

Air pollution injury to two species of the Sierra Nevada mixed-conifer type, namely, ponderosa pine *(Pinus ponderosa* Dougl. ex Laws.) and Jeffrey pine *(P. jeffreyi* Grev. & Balf.), has been evaluated along the western slope of the Sierra Nevada from Lake Tahoe to the region east of Bakersfield during the past 20 years (Miller and Millecan 1971, Peterson and others 1991, Stolte and others 1991). Injury to pines is due to elevated ozone concentrations in photochemical air pollution and is characterized mainly by chlorotic mottle symptoms leading to lower rates of photosynthesis and early loss of needles and, in extreme cases, by diminished annual ring width (Peterson and others 1987). Surveys have clearly identified the region east of Fresno, particularly the Grant Grove-Giant Forest areas, as having the most severe ozone damage to pines in the Sierra Nevada (Stolte and others 1991). Giant sequoia [*Sequoiadendron giganteum* (Lindl.) Buchholz] groves are commonly found within the mixed-conifer stands where pines show chronic injury.

Anecdotal evidence from natural giant sequoia groves in Sequoia and Kings Canyon National Parks and from giant sequoias planted in heavily polluted areas of the San Bernardino Mountains east of Los Angeles suggests no visible ozone injury to foliage of trees in the small sapling to mature size classes. Yet, lack of visible injury is not sufficient to indicate the complete absence of pollutant effects. Since decreased carbon fixation may result with or without apparent morphological injury to subcellular components in leaf tissue, gas exchange measurements provide important supporting evidence of the total effects of ozone. The sensitivity of plants to ozone may vary with foliage age or phenological stage, i.e., foliage of very young seedlings or very old, mature individuals may react differently, or actively growing tissue may be sensitive to injury when cold-hardened tissue may not be. Therefore it is important to use more than one indicator to evaluate plant sensitivity to air pollutants.

The uniqueness of giant sequoia among conifer species is based on its enormous size and longevity, its relatively small population size, and apparent ecological restrictions on grove boundaries (Rundel 1972). Its societal importance is shown by its protection in National Parks and State Parks in the Sierra Nevada. Because of these attributes, the possible influence of a new environmental stress factor such as air pollution requires thorough examination. The focus of air pollution effects research with giant sequoia has been on regenerative capacity, growth, and competitive relationships within the Sierra Nevadan mixed-conifer communities. The purpose of this paper is to review research carried out between 1983 and 1990 including (1) the results of experiments to test the visible injury and growth responses of seedling giant sequoias to ozone or ozone + sulfur dioxide in open-top fumigation chambers, (2) morphological responses and gas exchange responses of both seedlings and large saplings in fumigation experiments in Sequoia and Kings Canyon National Parks, and (3) the possible stand-level consequences of the chronic exposure of giant sequoia and companion tree species in native stands.

Air Pollution Effects on the Seedling Stage of Giant Sequoia

Beginning in 1982, the fumigation experiments conducted in open-top fumigation chambers at Riverside, California, included ozone and sulfur dioxide alone and in combinations (Taylor and others 1986). The inclusion of sulfur dioxide in this experiment was prompted by the State of California Air Resources Board's concern that sulfur

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dioxide concentrations in the southern San Joaquin Valley may be sufficient to interact with ozone to cause increased injury at downwind mountain sites. During 1977 and 1978 the maximum hourly ozone concentrations in the Bakersfield area ranged from 10 to 13 pphm (parts per hundred million) and were frequently accompanied by daily average sulfur dioxide concentrations of 5 to 7 pphm, particularly in April through October (Duckworth and Crowe 1979). After two years of ozone and sulfur dioxide monitoring at two Sierra Nevada locations it became apparent that ozone concentrations were usually similar to those in Bakersfield. However, mean maximum sulfur dioxide concentrations were only about 0.2 pphm at a typical mixed-conifer forest site (Shirley Meadow) in the Sierra Nevada northeast of Bakersfield (Miller and Stolte 1984).

Pollutant combinations are known to result in less-than-additive, additive, or more-than-additive (synergistic) injury to both herbaceous and woody species (Reinert and others 1975). A fumigation experiment carried out at Riverside from April 1 to June 2, 1982, included ozone at 0, 10, 20, 30, and 40 pphm alone, sulfur dioxide at 0, 5, 10, 15, 20 and 25 pphm alone, and ozone + sulfur dioxide combinations including 10+5, 10+10, 10+20, 20+5, 20+10, and 20+20 pphm (Taylor and others 1986). The experiment included ponderosa pine and Jeffrey pine seedlings aged 2-3 years and 4-month-old giant sequoia seedlings.

The visible injury response of each species, expressed as the percentage of the total leaf area *(table 1),* indicated that the greatest injury to ponderosa and Jeffrey pines resulted from 20 pphm ozone + 20 pphm sulfur dioxide, and from 40 pphm ozone. For giant sequoia, the exposure to 40 pphm ozone resulted in the highest observed values of visible injury, whereas mixtures of 10 or 20 pphm ozone with 20 pphm sulfur dioxide were associated with the 6th and 4th highest observed levels of injury. In this experiment, the exposure of giant sequoia to 10 pphm ozone alone did not result in injury significantly greater than the charcoal-filtered air control, and injury was not significant from ozone alone at 20 pphm.

The results of this work led to the question: Are giant sequoia seedlings injured in their natural forest environment by present ambient concentrations of ozone? This question was explored by fumigation of seedlings followed by evaluation of (1) histological examination of seedling foliage, (2) visible symptoms, (3) photosynthesis and respiration measurements, (4) biomass changes, and (5) seedling condition and mortality losses over a span of 4 years.

Ozone Exposure Experiments in Sequoia National Park

Biomass and Visible Injury Measurements

Fumigation experiments in open-top chambers were completed at Giant Forest in Sequoia and Kings Canyon National Parks in 1987 and 1988. Newly emerged giant sequoia seedlings, from seeds collected at the Giant Forest site, were grown in containers with natural soil. The containers were buried in order to prevent heating. From early June to late September seedlings were exposed to treatments

Table 1-*Percent,foliar injury response of 2- to 3-year-old ponderosa pine and Jeffrey pine and 4-month-old giant sequoia seedlings exposed to sulfur dioxide and ozone alone and in combinations from April 1, 1982 to June 2, 1982 (Taylor and others 1986)*

Ponderosa Pine			Jeffrey Pine			Giant Sequoia		
O_3	SO_2	Average injury	O_3	SO_2	Average injury	O_3	SO_2	Average injury
--pphm--		*--percent--*	*--pphm--*		*--percent--*	*--pphm--*		*--percent-*
20	20	57.40a	20	20	52.45a	40	0	91.60a
40	0	52.60ab	40	0	42.90a	20	10	79.80ab
20	10	48.60ab	20	10	40.40a	30	0	76.00abc
20	5	47.30ab	30	0	32.90ab	20	20	74.15abc
30	0	35.10 be	20	5	31.00ab	20	5	67.60abcd
10	20	21.20 cd	10	20	16.00 bc	10	20	63.20 bcde
20	0	16.55 cd	20	0	7.65 c	20	0	35.30 bcde
0	25	15.80 cd	10	10	6.40 c	0	20	35.10 bcde
10	10	8.40 d	10	5	5.10 c	10	5	32.30 cde
0	20	6.55 d	0	25	3.70 c	10	10	23.20 de
10	5	6.00 d	0	20	0.00 c	0	25	13.70 e
0	15	2.70 d	0	15	0.00 c	10	0	9.20 e
10	0	1.60 d	0	10	0.00 c	0	10	7.00 e
0	10	0.20 d	0	5	0.00 c	0	15	6.60 e
0	5	0.00 d	10	0	0.00 c	0	0	3.55 e
0	0	0.00 d	0	0	0.00 c	0	5	0.10 e

Upper bounds for pairwise comparison at $p = 0.05$, based on Tukey's multiple comparison method were ponderosa 22.09, Jeffrey 22.07, giant sequoia 46.13. Mean values of visible injury listed in columns are not significantly different if followed by the same lowercase letter.

including charcoal-filtered air, 1X ambient ozone within and outside chambers, and 1.5X ambient ozone in chambers. Treatments were replicated four times.

In 1987, the twelve chambers and four open plots were located on an old roadway so that no chambers or plots had shading from directly overhead. In spite of this attempt to obtain uniform sunlight, and no more than 2 hours of direct sunlight for all chambers and plots, one 1.5X and one ambient chamber received >4 hours during the first 30 days of the fumigation, and one filtered air chamber received more than 2 hours of direct sunlight per day during the entire fumigation. Because the durations of these exposures to sunlight greatly exceeded those received by other chambers, we decided to exclude them from the analysis because of the potential influence of duration of direct sunlight on response to ozone treatments. Analysis of root, shoot, and total weights of the harvested seedlings found no significant differences due to ozone exposure *(table 2).* Chambers as a random factor were always significant. Open plots were not included in the analysis (Miller and others 1988).

The second experiment completed in 1988 was at the same site except that the chambers and plots were moved to nearby sites under a more evenly distributed canopy of white fir [*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.], sugar pine *(P. lambertiana* Dougl.), and giant sequoia. The purpose was to attain lighting conditions more typical of seedbeds where giant sequoia seedlings commonly germinate and establish.

Table 2-*Dry weights of shoots and roots after exposure to 1 X ambient ozone in chambers and open plots and to 1.5X ambient ozone or filtered air in chambers from June 26 to September 24, 1987, at Giant Forest, Calif. The ANOVA was done on 12 of the 16 original chambers and plots in order to exclude one chamber in each treatment that had long durations of direct sunlight, namely, greater than 1.5 h day-I (Miller and others 1988).*

Treatment	Shoot weight	Root weight	Total weight	Root percent of total
	---------------g---------------			
I X Ambient Open	.0485	.0318	.0803	[1]-----
I X Ambient Chamber	.0452	.0311[2]	.0778	39.1
Filtered Air Chamber	.0459	.0325[2]	.0790	41.7
1.5X Ambient Chamber	.0387	.0202	.0589	33.2
Percent Difference[3]	-16	-38	-25	

[1]Value omitted intentionally since only within-chamber comparisons were being considered.
[2]Total weight is not always the sum of shoot and root weight averages because in a few cases the value for a shoot or root system was missing.
[3]*Filtered - 1.5X Ambient* X 100 = Percent Difference (Not significant, p=.05) Filtered

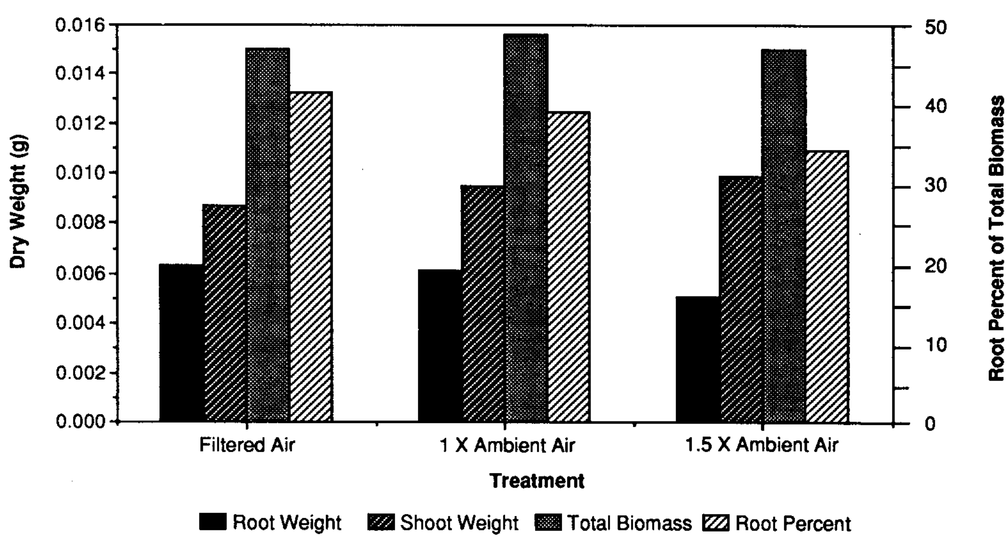

Figure 1-Distribution of plant weight into shoots and roots after exposure of containerized giant sequoia seedlings in natural soil following a 3-month exposure to ambient ozone (1X), 1.5X ambient ozone, and charcoal-filtered air at Giant Forest in 1988 (Miller and others 1991 a).

Seedlings harvested at the end of the 1988 fumigation showed effects on the weights of roots *(fig. 1)* that were not inconsistent with the results seen in 1987 *(table 2).* As in 1987, however, the ANOVA found no significant differences in root, shoot, or total plant weight due to ozone exposure. The experimental seedlings used in 1988 are illustrated in *figure 2.* These seedlings were selected at random from the harvested populations of each treatment. There appear to be fewer small feeder rootlets on seedlings exposed to 1.5X ambient ozone.

Our hypothesis was that there would be a decrease in the ratio of root weight to total plant weight as a result of exposure to 1.5X ambient ozone because the seedling may use carbon from the root system to repair foliar injury and thus decrease root development (Oshima and others 1979, Weinstein and Beloin 1990). Reduced root growth of giant sequoia seedlings was noticed in earlier fumigations completed in Riverside (Taylor and others 1986), but we were unable to detect any significant differences in 1987 or 1988.

The results for visible injury in 1988 (Miller and others 1991a) are representative of results in 1987. Amounts of chlorotic mottle or necrosis of cotyledonary and primary leaves were estimated in July, August, and September. These symptoms were essentially absent in trees exposed to filtered air, just detectable in ambient ozone treatments, and very prominent in 1.5X ambient ozone treatments *(fig. 3).*

Gas Exchange Measurements During the 1988 Experiment

The mechanism of ozone injury to seedlings and rooted cuttings was further characterized by measurements of gas exchange in situ (Grulke and others 1989). In this experiment, seedlings were asymptomatic in the charcoal-filtered chambers, but both asymptomatic and symptomatic in the 1.5X ambient ozone chambers. Rooted cuttings were asymptomatic at both ozone levels. Light response, respiration in the dark, and diurnal gas exchange of seedlings were characterized for asymptomatic seedlings in the charcoal-filtered chambers and for only symptomatic seedlings in the 1.5X ambient ozone chambers. For rooted cuttings the carbon dioxide (CO_2) exchange rate was measured under saturating light.

The principal results of this research are that the CO_2 exchange rate of symptomatic seedlings was significantly reduced (by 44 percent) relative to that of plants in charcoal-filtered chambers (n=8). The CO_2 exchange rate of rooted cuttings (all were asymptomatic) in the 1.5X ozone chambers was lower (by 20 percent), but differences were not statistically significant (n=5) compared to plants in the charcoal-filtered chambers *(fig. 4).* The decrease in CO_2 exchange rate in the seedlings could be explained principally by an increase in dark respiration rates for those plants exposed to elevated ozone. The light response was altered for seedlings in charcoal-filtered air versus 1.5X ambient ozone: light compensation point was greater, and CO_2 exchange rate at light saturation was lower for plants exposed to elevated levels of ozone. This result implies that if ambient ozone levels were to increase, seedlings may be less damaged by ozone on microsites with longer durations of higher intensity sun flecks that would permit them to gain enough carbon to compensate for ozone injury.

Gas Exchange Measurements of Ozone-Fumigated Branches of Giant Sequoia Saplings

The gas exchange results from seedlings and rooted cuttings led to the question: Are older giant sequoias affected in any detectable way by ambient or elevated ozone? We chose three large saplings, approximately 50 m tall and 120 years old, at a site within 200 m of the seedling fumigation experiments of 1987 and 1988 (midway between Giant Forest Village and Sunset Rock). Access to the upper crowns of these trees was provided by a scaffold. At about 30 m above the ground, branches were enclosed in chambers and exposed to either charcoal-filtered air or ozone at IX, 2X, and 3X ambient concentrations. One additional branch without a chamber was used as a control for chamber effects (statistically compared with the IX ambient treatment).

After exposure for both 1 and 2 months, there were no significant differences in gas exchange rate between chambered and unchambered branches at IX ambient ozone levels (Grulke and Miller 1993). Although not statistically significant, branches in subambient ozone chambers had a slightly higher CO_2 exchange rate than those in 1X, 2X, and 3X ambient ozone. This suggests that additional research should be directed toward increased replication and be focused on the subambient to ambient ozone levels. No significant effects were found on dark respiration, chlorophyll fluorescence, or water relations (pre-dawn and solar noon, total needle and osmotic + matric water potential) between the charcoal-filtered air, and 1 X, 2X, and 3X ambient ozone treatments.

In summary, sensitivity of giant sequoia to ozone declines from current year seedlings to rooted cuttings from 12-year-old seedlings (Grulke and others 1989). With foliage on 120-year-old trees, there were no significant differences in physiological characteristics across a wide range of ozone exposure levels. It may be, with the changing morphology of the needles (attached to older and older stems), that ozone entry into the needles becomes more limited or the foliage attached to older stems produces increasing amounts of anti-oxidants which destroys the ozone that does enter the leaf more effectively, or both. The maximum stomatal conductance declines with older trees, and mesophyll tissue becomes more compact.

Stand-Level Consequences of Chronic Ozone Exposure of Giant Sequoia Ecosystems

Seedling Condition and Survival in Natural Groves

Fumigation experiments, namely the assessment of visible symptoms, and photosynthesis after summer-long experiments have indicated that small seedlings are sensitive

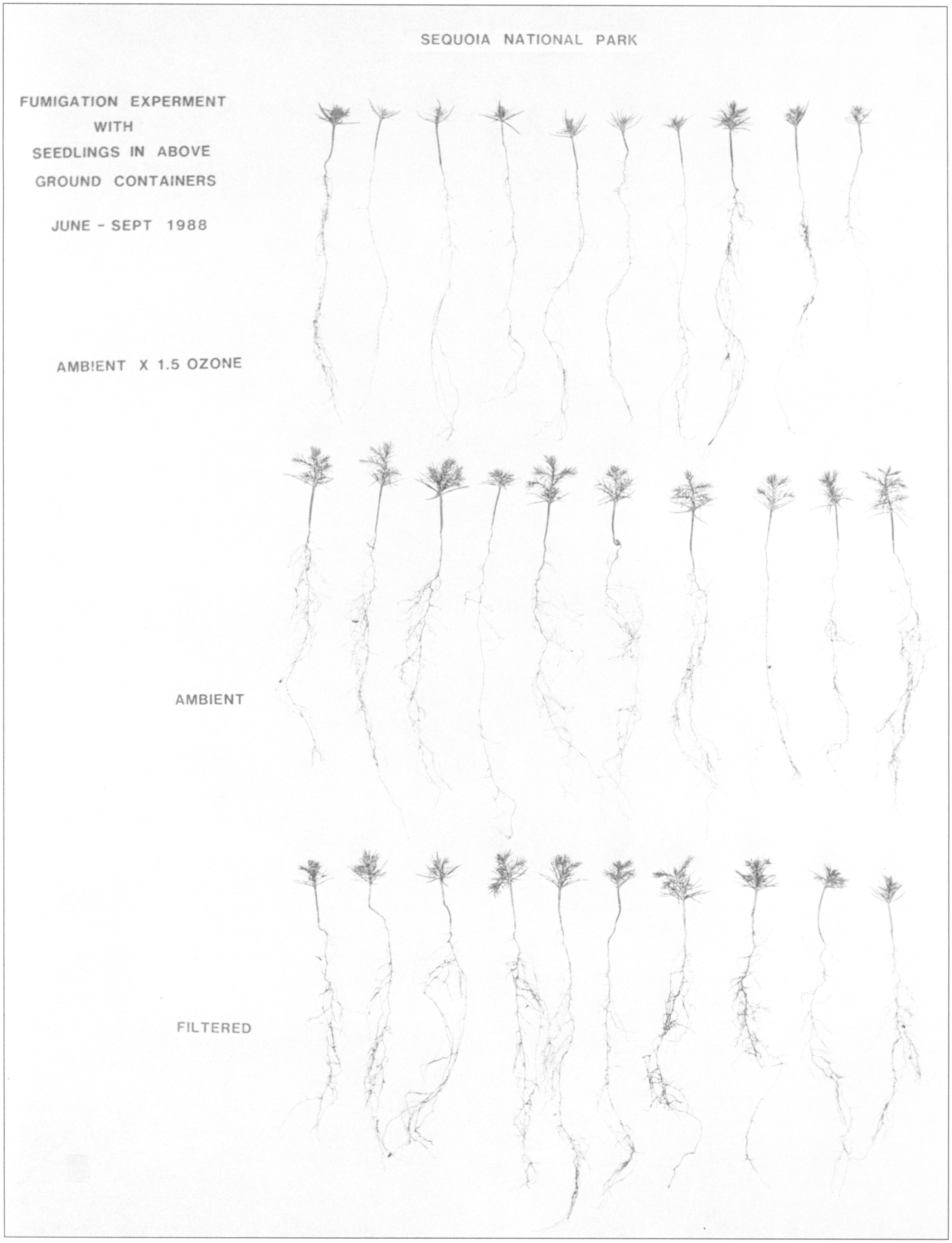

Figure 2-One set of several randomly selected samples of experimental seedlings after harvest 6 months after germination in 1988 from Sequoia National Park (Miller and others 1991 a).

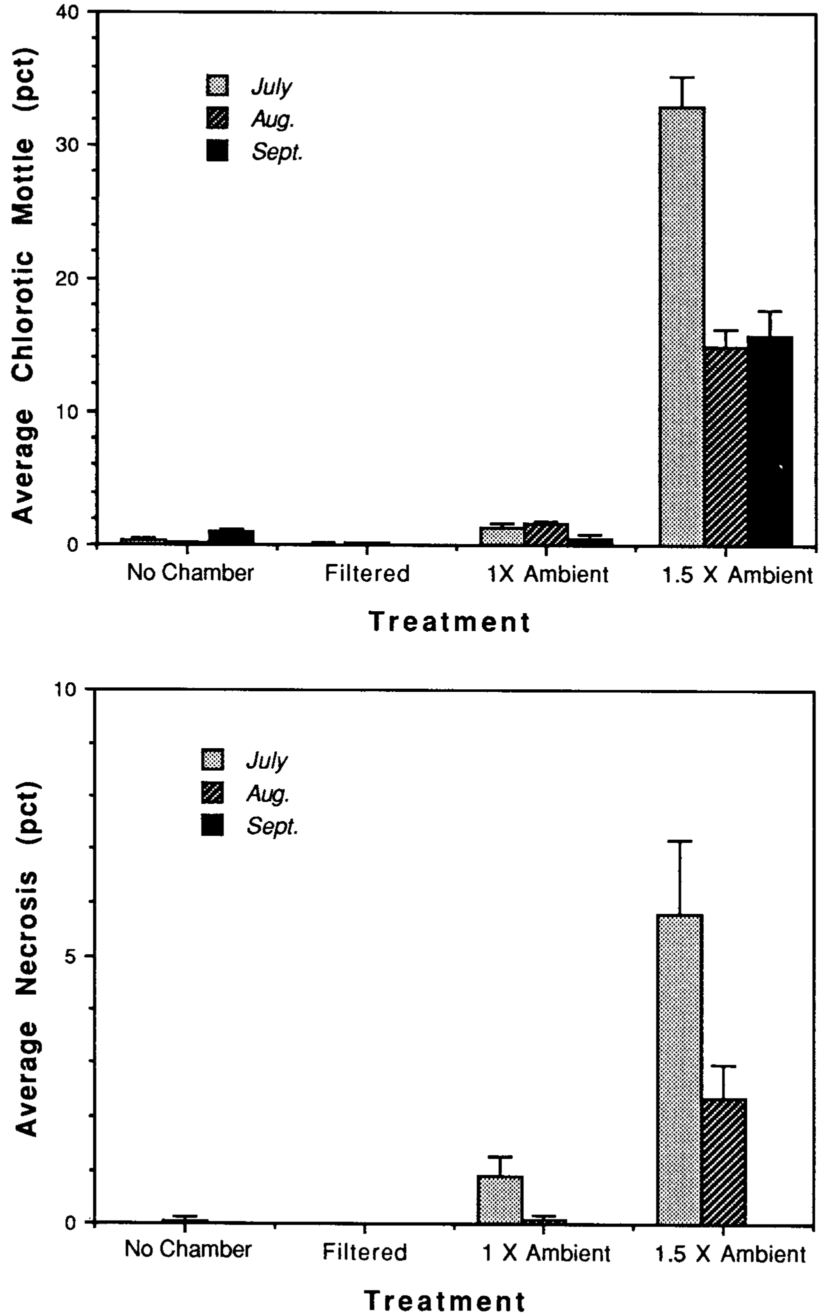

Figure 3-Estimates of the percent of total foliage surface area of giant sequoia seedlings with visible injury during exposure to ambient ozone (1X) or ambient ozone or charcoal-filtered air on July 10, August 8, and September 14, 1988 at Giant Forest (Miller and others 1991 a).

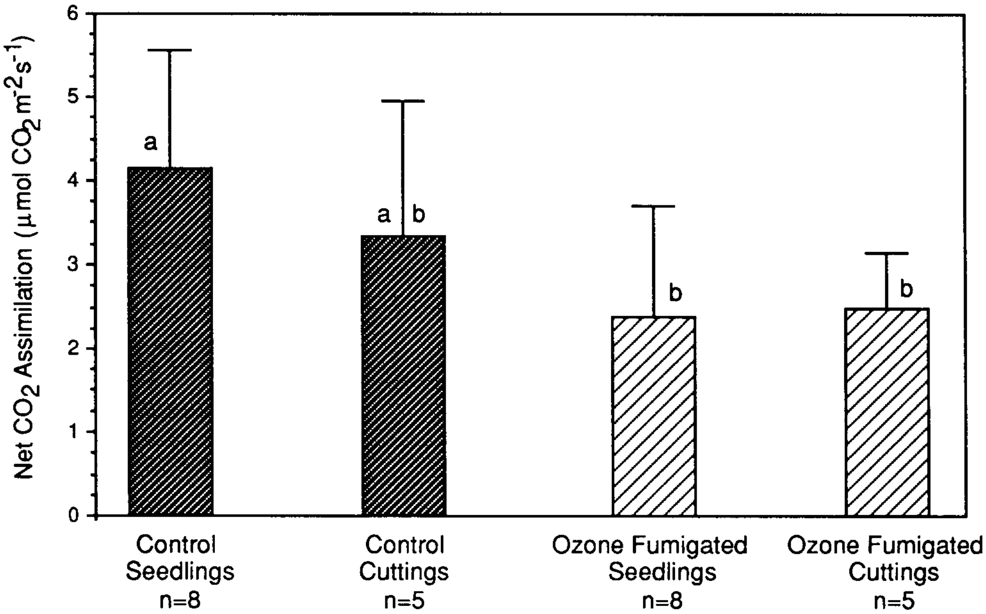

Figure **4**-Net CO_2 assimilation of giant sequoia seedlings and rooted branchlets from sapling giant sequoias after a 3-month exposure to charcoal-filtered air or 1.5X ambient ozone at Giant Forest in 1988 (Grulke and others 1989). Bars with the same lowercase letter (e.g., a,a or b,b) are not significantly different, p = 0.05.

after exposure to 1.5X ambient ozone during the first 3 months after emergence. An additional approach was taken to determine whether seedling injury by ozone was detectable in natural groves where recent prescribed fires had resulted in abundant regeneration. Randomly selected samples of primary needles from giant sequoia seedlings were collected in 1987 from three sequoia groves in Sequoia National Park and examined histologically (Evans and Leonard 1991). These results suggest that primary needles of seedlings from groves show histological evidence of ozone effects similar to those of needles from ozone fumigation experiments. Thus, present ambient levels of ozone exposure are sufficient to cause detectable ozone injury to recently emerged seedlings.

Seedling plots were established at nine locations in natural giant sequoia groves in 1983. At each location five 1-m[l] subplots were randomly selected from a 5- by 20-m grid. The appearances of symptoms and the mortality of seedlings were recorded in early and late summer each year from August 1983 to September 1986 (Miller 1987). A variety of leaf injury symptoms were observed that resulted in a gradual increase in the number of partially or wholly dead primary needles after which the seedlings died. There was no way to confirm that ozone was contributing to this symptom pattern. Seedlings that died early in the 3-year observation period had a uniform, light-straw-yellow color. It appeared that rapid desiccation had occurred because the root system had failed to become established. Many of the seedlings that died in the last year of observation had been buried by leaf and twig litter from nearby overstory trees. Between August 1983 and September 1986 at the nine plot locations, the seedling density decreased from an average of 12 seedlings to 2 seedlings per square meter.

Four of these plots had received a prescribed burn treatment in 1982, and the others had been burned between 1979 and 1981. The overwinter and summer mortality at four of the nine plots burned in 1982 is shown in *figure 5.* The seedlings at the General Grant Tree plot were growing on an extremely dry site with a very long daily duration of direct sunlight, and there was 42 percent mortality in the August 1983 to October 1983 period. Circle Meadow was a more mesic site, and mortality was not as rapid in the initial year. Three plots had less than 15 percent survival at the final observation, and one plot (General Grant Tree) had no survivors (Miller 1987).

Chronic Ozone Effects on Tree Species Competing with Giant Sequoia

It is clear from repeated surveys of ponderosa and Jeffrey pine plots in Sequoia and Kings Canyon National Parks that the most injury to these species is found in the Giant Forest-Grant Grove regions (Stolte and others 1991). There is some evidence that large-diameter Jeffrey pines on severe sites are showing a decline in annual ring growth that is related to crown condition (Peterson and others 1987). A similar study of ponderosa pines in the region failed to show any change in ring growth (Peterson and others 1991). Mortality of ponderosa and Jeffrey pines in the southern Sierra Nevada that is clearly related to ozone stress has not occurred as has already happened in the San Bernardino Mountains where ozone concentrations are higher. Other

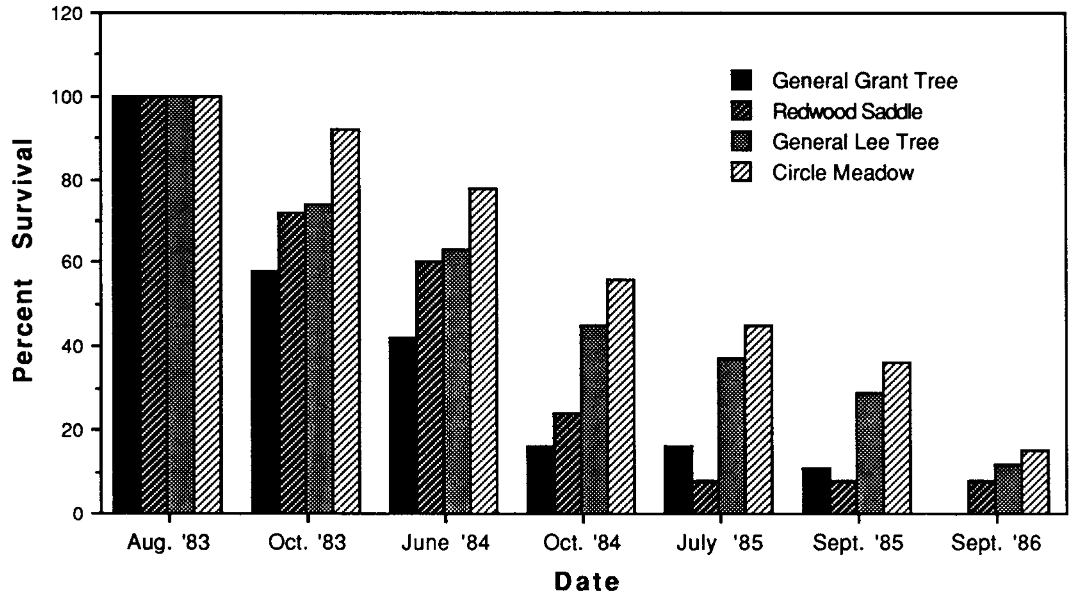

Figure 5-Survival of giant sequoia seedlings regenerated at four locations after prescribed burns in 1982. Survival counts were made in mid and late summer from August 1983 to September 1986 (Miller 1987).

companion species including white fir, sugar pine, incense cedar [*Calocedrus decurrens* (Tory.) Florin], and California black oak *(Quercus kelloggii* Newb.) are more tolerant to ozone. These species have shown generally larger increases in basal area than ponderosa or Jeffrey pines at plots in the San Bernardino National Forest where ozone exposure levels are nearly double those found in Sequoia and Kings Canyon National Parks (Miller and others 1991b). It is prudent to be vigilant for ozone-induced interspecific competitive changes in the southern Sierra Nevada mixed-conifer forests that could have an influence on well-established giant sequoias and the success of new seedling establishment.

Discussion

The objectives of this work were centered around the question: Is any age class of giant sequoia injured directly by ambient ozone levels currently measured or potentially possible in the atmosphere at Sequoia and Kings Canyon National Parks? Several lines of evidence indicated that symptoms of ozone injury are detectable on seedling foliage in natural groves in the first months after emergence. Two field fumigation experiments had consistent results; however, shoot, root, and total plant weights of fumigated seedlings were not significantly different from those of seedlings in charcoal-filtered air after exposures to 1.5X ambient ozone for 3 months. Visible symptoms of ozone injury were very prominent in seedlings treated with 1.5X ambient ozone in both experiments.

Seedlings growing in microsites with short durations of direct sunlight may be more at risk from ozone injury because insufficient light would not permit compensation for the reduced photosynthesis and increased respiration caused by ozone injury (Grulke and others 1989). Successful development of root systems to depths sufficient to reach subsoil moisture and thus avoid the typical summer drought is essential for survival in the first season of growth. If ozone injury leads to reduced root development (Oshima and others 1979), it is possible that seedling survival could be curtailed in an environment of deteriorating air quality.

In past centuries, giant sequoia has not been exposed to elevated ozone concentrations (Kasting 1993); therefore, there would have been no opportunity for natural selection of tolerant individuals. Instead, fire and drought are generally recognized as the principal selective agents for seedlings. Our observations in natural groves between 1983 and 1986 showed an average reduction in seedling density from 12 to 2 seedlings per square meter. If ozone air quality should deteriorate more, it is possible that ozone could act as a new selection pressure during the early seedling stage. Genotypes that may be eliminated by ozone selection may have important attributes that contribute to the future success of the species.

For the large sapling stage of giant sequoia, the measurement of photosynthesis and other physiological parameters did not reveal any impairment after exposure for 2 months to concentrations up to 3X ambient ozone. Ponderosa and Jeffrey pines would have been very seriously damaged by such a treatment. These results of sapling fumigation are supported by observations of vigorous health of giant sequoias growing in the San Bernardino Mountains at seasonal ozone concentrations that approach 2X the ambient concentration in the Sierra Nevada.

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