

LENDING Slips
University of Alaska Fairbanks ILL



ILLiad TN: 375319

LENDING REQUEST

TN: 375319

Borrower: NMW

Lending String:

GZM,RLA,*UAF,CUY,DLC,NTD,UIU,MEU,EYM,C
OO

Patron:

Journal Title: Proceedings of the ... North
American Forest Biology Workshop.

Volume: **Issue:**

Month/Year: 1986 **Pages:** 3

Article Title: Population changes in eastern
hardwoods caused by air pollution.

Article Author:

ILL Number: 177058599



Call #: SD395.N67 1986

Location: Level 5

Request Date: 5/3/2017 2:50:33 PM

Shipping Address:

INTERLIBRARY LOAN DEPT
HUNTER LIBRARY/WCU
176 Central Drive
Cullowhee, North Carolina 28723
United States

Fax: 828-227-7380

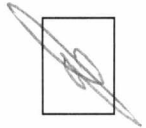
Ariel: 152.30.6.124

Email: libraryloan@email.wcu.edu

Attention:

ODYSSEY: 206.107.43.191

Initial when Updated to Found:



POPULATION CHANGES IN EASTERN HARDWOODS CAUSED BY AIR POLLUTION

P. Berrang, D.F. Karnosky, R.A. Mickler, and J.P. Bennett¹

Abstract -- Evolution of ozone tolerance can provide indirect evidence that air pollution is reducing growth of forest trees. Acer rubrum from natural populations in nine national parks and Populus tremuloides from natural populations in five national parks were fumigated to determine ozone tolerances. Ozone tolerances of P. tremuloides populations from high and intermediate ozone areas were greater than ones from low ozone areas. A. rubrum populations from areas with historically high ozone concentrations showed more tolerance than those from low or historically low ozone areas. These results suggest air pollution is reducing the reproductive fitness of some individuals in relatively polluted areas.

Air pollution has been implicated in reduction of growth of several tree species in the eastern United States (Jensen 1982, Wang *et al.* 1986). Ozone is the most widely distributed of all air pollutants at known phytotoxic concentrations (Heck 1984). Eastern hardwoods are exposed, in parts of their ranges, to higher than natural background levels of ozone and are a likely candidate for ozone-induced changes in the genetic makeup of natural populations.

Genetic variation in ozone tolerance would be a prerequisite for an ozone-induced population change. Variation in this trait has been shown to exist within one population of quaking aspen, Populus tremuloides Michx., (Karnosky 1977) and within and among many populations of green and white ash, Fraxinus pennsylvanica Marsh. and F. americana L. (Karnosky and Steiner 1981). One objective of this study was to test populations from each of several additional species of eastern hardwoods to determine whether genetic variation for ozone tolerance is common among eastern hardwood tree species.

There should be a gradual increase in the average ozone tolerance of populations of trees in areas with high concentrations of ambient ozone if variation in ozone tolerance is indicative of differences in reproductive fitness in the presence of ozone. Data that indicate populations from high ozone areas are more tolerant than populations from low ozone areas when grown in a common environment can provide indirect evidence that this pollutant has already adversely affected some populations of trees. A second objective of this study was to examine this sort of evidence for several species of eastern hardwoods.

MATERIALS AND METHODS

Four to 14 individuals from each of five populations of quaking aspen and nine populations of red maple (Acer rubrum L.) growing in national parks that differed considerably in air quality (Table 1) were sampled for this

¹Research Scientist and Professor, Michigan Technological University, Houghton, MI; Forest Scientist, Northrop Services, Inc. Research Triangle Park, NC; and Ecologist, National Park Service, Denver, CO.

Table 1 - Locations of populations from which clones of various eastern hardwoods were collected and the average annual ozone concentrations at those locations.

Population origin	Number of clones of each species propagated at each location				Average annual ozone concentration *
	<u>Populus tremuloides</u>	<u>Acer rubrum</u>	<u>Cornus florida</u>	<u>Prunus serotina</u>	
Cuyahoga Valley National Recreation Area, Ohio	10	4			65 ppb
Shenandoah National Park, Virginia		10	3	11	49
Great Smoky Mountains National Park, Tennessee		14	8	6	47
Mammoth Cave National Park, Kentucky		10	8	5	67
Buffalo National River, Arkansas		8	8	8	53
Saratoga National Historical Park, New York	13	12		5	49
Acadia National Park, Maine	14	8		4	52
Isle Royale National Park, Michigan	12	4			14
Voyageurs National Park, Minnesota	14	7			26

*Annual average of maximum daily one hour averages. For each park, the year data was collected; US EPA SAROAD sitecode, Canadian NAPS station, or location of monitor used; and distance and direction from park are listed.

Cuyahoga: 1983, SAROAD 360060020H01, 3 km SE
 Shenandoah: 1984, SAROAD 482890003N05, in park
 Gt Smoky Mts: 1983, SAROAD 441190101F03, in park
 Mammoth Cave: 1983, SAROAD 183140005F01, 90 km NW
 Buffalo River: 1983, Average of SAROAD 041880002F01 and 373020174F03, 130 km S and 247 km W, respectively
 Saratoga: 1983, SAROAD 336020003F01, 34 km SW
 Acadia: 1983, SAROAD 200010003F05, in park
 Voyageurs: 1983, Atikokan, Ontario, 100 km
 Isle Royale: 1983, NAPS 60806R, 50 km W

study. In addition, three to eleven individuals from populations of black cherry, Prunus serotina Ehrh., in six national parks and populations of flowering dogwood, Cornus florida L., from four national parks were collected from areas with intermediate or relatively high levels of ozone. All individuals were sampled without regard to size, form, or symptoms of ozone injury and were separated by at least 100 m, but not more than 15 km. These individuals were vegetatively propagated and grown in the greenhouse.

The relative ozone tolerances of the various clones was determined by exposing them to ozone doses shown to induce a broad range of injury in preliminary fumigations (Table 2). All trees were moved from a cold storage facility to a greenhouse in early March and fumigated in May to avoid extra-fumigation exposure to elevated levels of ambient ozone. A randomized complete block design with non-contiguous plots within replicates was used. Each aspen replicate was fumigated on a separate day, but all replicates of each of the other three species were fumigated together. A 2.4 m tall by 4.6 m diameter plastic chamber located in a greenhouse was used for fumigations. Air was charcoal filtered and passed through a duct where ozone was generated with ultra-violet lamps before it entered the fumigation chamber. Ozone concentrations were continuously monitored with a Dasibi Model 1003 Ozone Analyzer and rarely deviated more than 5% from desired levels. Because we were interested in determining relative amounts of injury among large numbers of genotypes within a short amount of time, ozone response was evaluated by visible injury.

Table 2 - Ozone concentrations used to test populations of four eastern hardwood species for within population variation in ozone tolerance and average injury observed for all populations within each species.

Species tested	Ozone exposure			Average injury class ¹
	pphm ozone	No. hrs/day	No. days	
<u>Populus tremuloides</u>	18	6	1	1.8
<u>Prunus serotina</u>	25	6	1	1.7
<u>Acer rubrum</u>	25	8	3	.5
<u>Cornus florida</u>	25	8	3	.1

¹ Injury class can range from 0 (no injury) to 5 (severe injury on all leaves).

Symptoms were allowed to develop seven days for quaking aspen and black cherry and ten days for red maple and flowering dogwood. Then the percentage of leaves injured and the leaf area injury class of injured leaves (0 = no injury, 1 = 1-20%, ... , 5 = 81-100%) was determined for each tree. The average leaf area injury class for all leaves was calculated for each tree. This is similar to the severity index developed by Davis and Coppolino (1974). Data were analyzed using standard methods of analysis of variance.

RESULTS AND DISCUSSION

Differences in visible injury among the four species corresponded well to published information on their relative ozone sensitivities (Davis *et al.* 1981, Davis and Gerhold 1976). Quaking aspen, which is generally recognized as ozone sensitive, was exposed to the lowest ozone dose and showed the greatest amount of ozone injury. Red maple and flowering dogwood, both considered ozone tolerant, received the highest ozone dose and showed the lowest amounts of injury. Black cherry received an intermediate ozone dose and displayed intermediate levels of injury (Table 2).

Differences among individuals within populations were sizeable for all four species. In almost every population the percentage of leaves injured on the most sensitive clone was twice that of the most tolerant clone and in some cases the differences in percentage of leaves injured was more than twenty-fold. A wide range of ozone tolerances were observed even in the relatively polluted parks and for the more ozone sensitive species. In all cases that could be tested, variation among clones within a population accounted for a larger portion of the variance than variation among populations.

The primary interest in this study was to determine whether there were differences in ozone tolerance between populations of trees in high ambient ozone areas and low ambient ozone areas. Population samples were obtained from areas that differed in air quality for two species, red maple and quaking aspen (Table 1).

Quaking aspen from the most polluted park sampled were considerably more tolerant of ozone than those from the most pristine parks sampled. Fifty percent more of the leaves on trees from Isle Royale and Voyageurs National Parks showed symptoms of ozone injury than on trees from Cuyahoga Valley National Recreation Area (Table 3). The average leaf area injury class for trees from the most polluted park was about half that of those from the least polluted park (Table 4). The 1983 and 1984 ozone data in Table 1 did not necessarily reflect historical levels of ozone, but the significant correlation ($r = -0.95$ $P=0.013$) between the average leaf area injured and the average annual ozone concentration suggested a close relationship between the two variables. Differences in injury among the five parks, as judged both by percentage of leaves injured and average leaf area injury, were highly statistically significant ($P = 2 \times 10^{-5}$ and 2×10^{-4} , respectively). These results are very similar to those obtained the previous year with the same collection of plant material (Table 5). They are consistent with the hypothesis that natural selection for ozone tolerance has occurred in populations of quaking aspen in polluted areas. Although injury to populations from parks with intermediate levels of ozone were not significantly different from those of either high or low ozone parks, the fact that they were intermediate and the strong correlation between ambient ozone and injury suggests that selection for ozone tolerance may be occurring in these parks as well.

Large differences in injury were found among populations of red maple from the nine national parks where this species was collected. The percentage of leaves injured and the average leaf area injury class for trees from the most sensitive population was more than twice that for trees from the most tolerant population (Tables 6 and 7). The three populations

Table 3 - Percentage of leaves showing visible injury for two-year-old clones of quaking aspen from populations in five national parks that were fumigated with 18 pphm ozone for six hours.

<u>Population origin</u>	<u>Population mean*</u>	<u>Range of clonal means</u>	<u>No. of clones</u>
Cuyahoga Valley NRA	50% a	21 - 63%	10
Saratoga NHP	58 ab	35 - 83	13
Acadia NP	60 ab	22 - 84	14
Voyageurs NP	71 bc	60 - 82	14
Isle Royale NP	75 c	58 - 88	12

* Populations followed by the same letter are not significantly different ($P \leq .05$) from each other.

with the lowest percentage of leaves showing visible injury included one from a park with a relatively high level of ozone, Cuyahoga Valley National Recreation Area and two with intermediate levels of ozone, Great Smoky Mountains and Shenandoah National Parks. The population from Cuyahoga Valley National Recreation Area was also relatively ozone tolerant in the quaking aspen study. The relative amounts of injury among the remaining six populations did not appear to be related to differences in ambient ozone at the parks of origin. Differences among the nine populations, as determined by both percentage of leaves injured and average leaf area injury class, were not statistically significant ($P = .102$ and $.157$, respectively) when the effect of clone within park was included in the model, but were highly significant ($P = 2 \times 10^{-6}$ and 5×10^{-5}) when it was dropped from the model.

Table 4 - Average leaf area injury class* for all leaves on two-year-old cuttings of quaking aspen from populations in national parks that were fumigated with 18 pphm ozone for six hours.

<u>Population origin</u>	<u>Population mean**</u>	<u>Range of clonal means</u>	<u>No. of clones</u>
Cuyahoga Valley NRA	1.1 a	0.2 - 2.3	10
Saratoga NHA	1.4 ab	0.5 - 2.9	13
Acadia NP	1.7 ab	0.2 - 3.2	14
Voyageurs	2.3 b	1.0 - 3.8	14
Isle Royale	2.3 b	0.6 - 4.1	12

* Average leaf area injury class could range from 0 (no injury) to 5 (severe injury on all leaves).

** Populations followed by the same letter are not significantly different ($P \leq .05$) from each other.

Table 5 - Percentages of leaves showing visible injury for one-year-old clones of quaking aspen from populations in five national parks that were fumigated with 18 pphm ozone for six hours.

<u>Population origin</u>	<u>Population mean</u>	<u>Range of clonal means</u>	<u>No. of clones</u>
Cuyahoga Valley NRA	38%	21 - 62	11
Saratoga NHP	47	15 - 72	14
Acadia NP	49	24 - 73	15
Voyageurs	45	20 - 62	12
Isle Royale	54	27 - 65	15

These results support our hypothesis that natural selection for ozone tolerance is occurring in relatively polluted parks. Because red maple is more tolerant of ozone than quaking aspen it is reasonable to expect that

Table 7 - Average leaf area injury class* for all leaves on clones of red maple from populations in nine national parks that were fumigated with 25 pphm ozone for eight hours per day on three consecutive days.

<u>Population origin</u>	<u>Population mean**</u>	<u>Range of clonal means</u>	<u>No. of clones</u>
Shenandoah NP	0.29 b	0.06 - 0.68	10
Cuyahoga Valley NRA	0.32 b	0.00 - 0.65	4
Great Smoky Mts. NP	0.35 b	0.02 - 0.67	14
Voyageurs NP	0.41 ab	0.14 - 1.12	7
Isle Royale NP	0.45 ab	0.03 - 0.71	4
Saratoga NHP	0.50 ab	0.11 - 1.25	12
Mammoth Cave NP	0.53 ab	0.23 - 1.11	10
Buffalo NR	0.61 ab	0.17 - 0.98	8
Acadia NP	0.68 a	0.26 - 1.30	8

* Average leaf area injury class could range from 0 (no injury) to 5 (severe injury on all leaves).

** Populations followed by the same letter are not significantly different ($P \leq .05$) from each other.

The effect of ozone on the vegetation in these parks is likely more severe than visible symptoms in the field would suggest. The influence of man has increased ozone levels at even the most polluted parks sampled, only within perhaps the last 60 to 80 years (Treshow 1980), a relatively short time in terms of tree generations. Selection for ozone tolerance would have to be extremely intense to produce the changes described here in such a short amount of time. The ambient ozone levels at even the relatively high ozone parks sampled were considerably lower than those in the most polluted parts of the United States. Presumably selection for ozone tolerance would be even more intense in areas with levels of ambient ozone higher than those sampled in this study.

REFERENCES

- Berry, C.R. 1964. Differences in concentrations of surface oxidant between valley and mountaintop conditions in the southern Appalachians. J. Air. Pollut. Control Assoc. 14: 238-239.
- Berry, C.R. and G.H. Hepting. 1964. Injury to eastern white pine by unidentified atmospheric constituents. For. Sci. 10: 2-13.
- Berry, C.R. and L.A. Ripperton. 1963. Ozone, a possible cause of white pine emergence tipburn. Phytopathology 53: 552-557.
- Davis, D.D. and J.B. Coppolino. 1974. Relative ozone susceptibility of selected woody ornamentals. HortScience 9: 537-539.
- Davis, D.D. and H.D. Gerhold. 1976. Selection of trees for tolerance of air pollutants. In: F.S. Santamour, Jr., H.D. Gerhold, and S. Little (eds.) Better Trees for Metropolitan Landscapes. U.S. Dept. Agric., For. Serv., Gen. Tech. Rep. NE-22. pp. 61-66.
- Davis, D.D., D.M. Umbach, and J.B. Coppolino. 1981. Susceptibility of tree and shrub species and response of black cherry foliage to ozone. Plant Disease 65: 904-907.
- Gschwandtner, G., K. Gschwandtner, K. Eldridge, C. Mann and D. Mobley. 1986. Historic emissions of sulfur and nitrogen oxides in the United States from 1900 to 1980. J. Air Pollut. Cont. Assoc. 36: 139-149.
- Heck, W.W. 1984. Defining gaseous pollution problems in North America. In: M.J. Koziol and F.R. Whatley, Gaseous Air Pollutants and Plant Metabolism. Butterworths, Boston. pp. 35-48.
- Jensen, K.F. 1982. An analysis of the growth of silver maple and eastern cottonwood seedlings exposed to ozone. Can. J. For. Res. 12: 420-424.
- Karnosky, D.F. 1977. Evidence for genetic control of response to sulfur dioxide and ozone in Populus tremuloides. Can. J. For. Res. 7: 437-440.
- Karnosky, D.F. and K.C. Steiner. 1981. Provenance and family variation in response of Fraxinus americana and F. pennsylvanica to ozone and sulfur dioxide. Phytopathology 71: 804-807.
- Treshow, M. 1980. Pollution effects on plant distribution. Environmental Conservation 7: 279-286.
- Wang, D., D.F. Karnosky, and F.H. Bormann. 1986. Effects of ambient ozone on the productivity of Populus tremuloides Michx. grown under field conditions. Can. J. For. Res. 16: 47-55.

BIOMASS PRODUCTION AND NUTRIENT RESPONSES OF PONDEROSA PINE
TO LONG-TERM ELEVATED CO₂ CONCENTRATIONS^{1/}

Jeremy S. Fried^{2/}, Kris A. Surano^{2/}, Paul F. Daley^{2/},

Joseph H. Shinn^{2/} and Paul Anderson^{3/}

Abstract.--Ponderosa pine saplings and seedlings were continuously exposed to elevated CO₂ concentrations of ambient, and ambient +75, +150, and +300 ppm in open-top chambers for 27 months. Saplings responded by reducing above ground biomass production. Although potassium concentration in both saplings and seedlings diminished as CO₂ concentration increased, no nutrients appeared to become limiting to growth as a result of elevated CO₂. Concentrations of Ca, Mg and Zn in the saplings at different concentrations of CO₂ mirrored root densities, indicating that an increase in root density at +150 ppm may account for greater nutrient concentrations observed in that tree.

Additional Keywords: *Pinus ponderosa*, x-ray densitometry, carbon dioxide.

This study is part of a long-term fumigation experiment conducted at the Lawrence Livermore National Laboratory that examined the morphological, phenological and growth effects of elevated CO₂ concentrations on ponderosa pine (*Pinus ponderosa* Laws.) saplings and seedlings (Surano *et al.*, 1986). This paper describes the growth responses by the pine saplings and the nutrient responses by both saplings and seedlings. Seedling growth is described in these proceedings by Houpis *et al.* (1986).

Several studies have been conducted to determine individual plant species' responses to elevated CO₂ concentrations (Lemon, 1983; Kimball, 1983). In general, forest tree species have responded to short-term exposures by increasing height growth, stem basal diameter growth, leaf area, photosynthetic rates and biomass production and by reducing stomatal conductance and transpiration (Tolley and Strain, 1984,; Higginbotham *et al.*, 1985; Sionit *et al.*, 1985; Rogers *et al.*, 1980, 1983). This study of the effects of elevated atmospheric CO₂ concentrations on ponderosa pine is the first to be performed *in situ* on entire trees for longer than one growing season, and was designed to determine whether previously reported responses to short-term exposures would continue, or whether acclimation might occur. The growth conditions were unique among related studies because we used open-top chambers and levels of CO₂ that can realistically be expected to prevail globally within the next 80 to 100 years.

^{1/} Work performed under the auspices of the U.S. Department of Energy by the Lawrence Livermore National Laboratory under contract W-7405-ENG-48. The authors acknowledge Robert Palassou and Jill DeGrange for their contributions.

^{2/} Environmental Sciences Division, Lawrence Livermore National Laboratory, P.O. Box 5507, Livermore, CA 94550.

^{3/} Department of Forestry and Resources Management, University of California, Room 145 Mulford Hall, Berkeley, CA 94720.

An increase in short-term photosynthetic rate doesn't assure increased long-term growth unless sufficient water and nutrients are available (Kramer, 1981). Since tree growth in temperate forests is often limited by nitrogen and/or phosphorous (Lavender and Walker, 1979) it is conceivable that mineral nutrition could limit the magnitude or tenure of CO_2 -induced growth-rate enhancement. Thus, while ambient concentrations of CO_2 may limit growth, elevated CO_2 will increase yields only until further increases in growth are precluded by insufficient quantities of some other plant requirement.

Increases in biomass of Virginia pine seedlings, particularly in roots, have been demonstrated with short-term exposures (Luxmoore *et al.*, 1986). In our long-term study, biomass of needles, buds, branches, boles and roots was measured at the end of the experiment, after 27 months of continuous fumigations. Changes in needle biomass and leaf area could have significant effects on water and nutrient use and these changes might affect the productivity of marginal sites. Though a small contribution to total biomass, the weight of buds is an excellent indicator of future growth.

METHODS

We measured biomass and conducted foliar-nutrient analyses on 4 ten-year-old ponderosa pine saplings and 16 potted (4 L pots) four-year-old Rocky Mountain ponderosa pine seedlings (var. *scopulorum*) growing in open-top chambers that had been continuously subjected to atmospheric CO_2 concentrations of 340-640 ppm from July 1983 through September 1985 (Surano *et al.*, 1986). The four treatments were ambient (+0), ambient + 75 ppm (+75), ambient + 150 ppm (+150) and ambient + 300 ppm (+300). Both seedlings and saplings received supplemental irrigation throughout the dry season at intervals frequent enough to preclude moisture stress and, in addition, the seedlings were fertilized monthly with a horticultural formulation that contained 2.9 g N, 2.3 g P, 1.7 g K, 1.7 g S, 0.9 g Ca and 0.3 g Fe per seedling.

Ten 2-g needle samples from the 1984 and 1985 age classes were collected from each seedling and three 2-g needle samples from these age classes were collected from each of four seedlings in each chamber on September 22, 1985, at the end of the experiment. All samples were immersed in liquid nitrogen immediately after collection, stored on dry ice, freeze-dried and then ground to pass a #20 mesh. One sub-sample of each sample was analyzed for total nitrogen by the micro-Kjeldahl method outlined by Bremner (1965) and another was ashed and analyzed for P, K, S, Ca, Mg, Mn, Fe, Cu, B, and Zn by plasma emission spectroscopy as described by Jones (1977).

At the conclusion of the experiment, both seedlings and saplings were dissected and their biomass partitioned by plant part and age class before drying and weighing. All plant parts were dried at 70°C . Needles were grouped by age class. On the saplings, branches were cut at each node and bulked by the age of the oldest wood accumulated in the branch segment. The main stems were also cut at each node and weighed. In addition, a 5-mm-thick slice of wood was removed from the basal end of each bole segment for densitometric analysis.

Tree-ring densitometry was conducted using a scanning x-ray densitometer of the type described by Echols (1970) to determine wood density and volume for each age class of wood (Figure 1). The earlywood and latewood widths and average earlywood and latewood densities were calculated for each annual ring

for each stem segment of each sapling. The volume increment of both early and latewood from each age class of wood was calculated by difference using Huber's formula (Husch et al., 1972) under the assumption that conic frustrums best described the volumes of these stem segments. Biomass was calculated as the product of density and volume for each wood type from each wood age class and was aggregated by wood age class over the entire stem. The estimated biomass by vertical stem section was aggregated to permit comparison with the corresponding biomass values determined directly by weighing. To estimate the biomass in each conic sheath of wood on each stem segment, we adjusted our densitometrically determined biomass values for each section by the actual weight for that stem section.

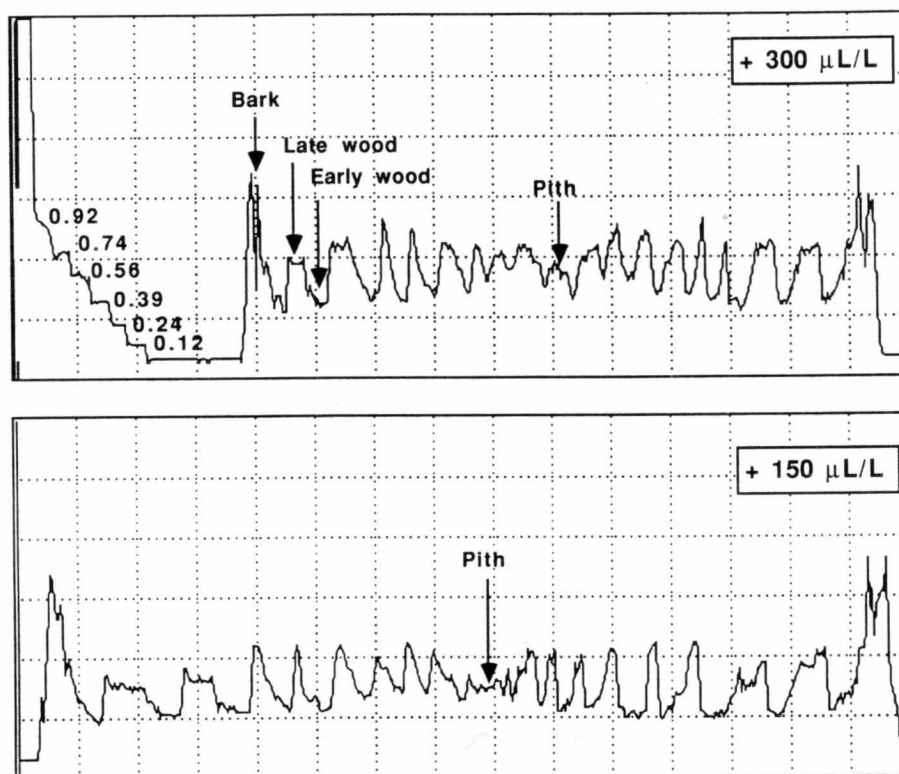


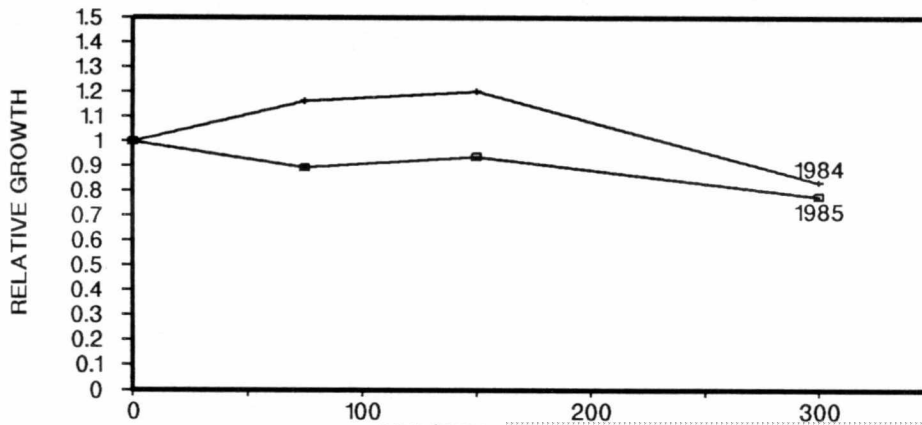
Figure 1. X-ray densitometry scans of stem cross sections from the base of the saplings growing under +150 and +300 ppm above ambient CO_2 . Numbers next to the steps of the calibration wedge represent the densities of wood (g/cm^3) that correspond to those steps. The arrows point to earlywood and latewood produced in 1984. Note the difference in size of the most recent ring widths of these trees.

Mean element concentrations were calculated for each needle age class for each sapling. A nested ANOVA was performed on the seedling data, with seedlings nested within chamber.

RESULTS

Biomass of Saplings

Wood density varied somewhat among trees but remained essentially unchanged within each tree over the 4-year period 1982 to 1985 in both treatments and controls. Average earlywood density for all trees during this period was 0.36 g/cm^3 , range 0.30-0.44, and average latewood density was 0.56 g/cm^3 , range 0.46-0.64. Absolute stemwood biomass increment over the two-year period 1984-85 varied considerably among treatments, from 2.6 to 5.1 kg; however, since the initial sizes of these trees were not equal, relative growth (current year's stemwood biomass increment/ previous year's stemwood biomass increment) was a more appropriate index of comparison. Relative growth for all trees increased from 1982 to 1983, most likely in response to irrigation, and then declined in both 1984 and 1985 as the previous stemwood biomass increment term became large. When the effects of the treatments on relative stem growth were normalized to the control tree (Figure 2), it became apparent that in 1984, the +75 and +150 treatments showed greater relative growth than the control, but the tree at +300 ppm grew relatively less. In 1985, the trees at intermediate treatment levels performed more poorly than the control and the tree at +300 ppm again grew even less.



Litterfall was not collected; therefore, the reduction in needle biomass may be partly explained by premature needle abscission that was observed. However, shorter needle lengths were observed on the +300 sapling during the final year and may have also contributed to the reduction in needle biomass. Specific leaf area ranged from 82 to 113 cm²/g for the 1985 needles and from 78 to 97 cm²/g for the 1984 needles, and there were no apparent trends related to CO₂ concentration.

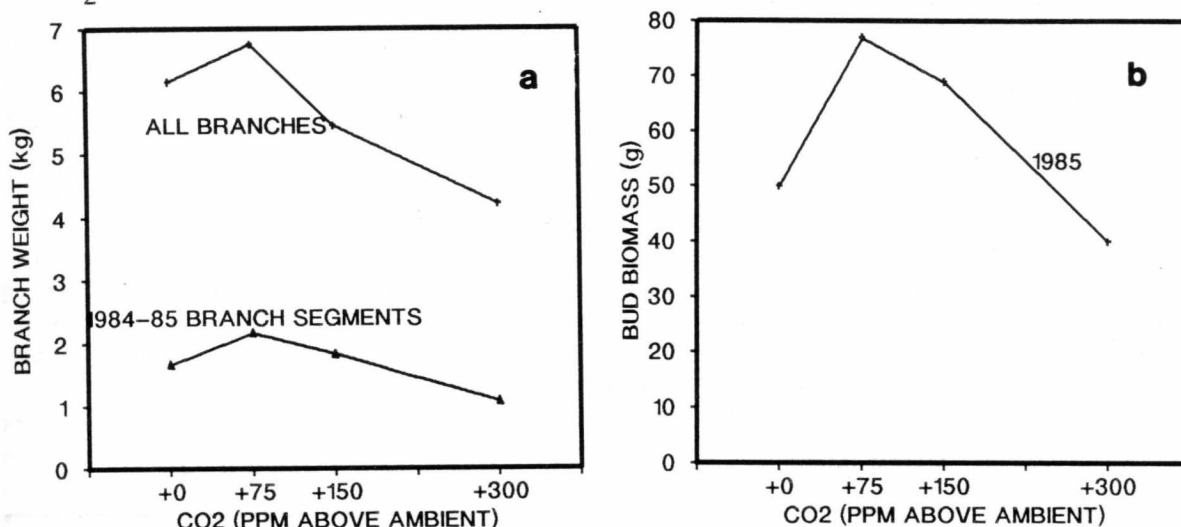


Figure 3. a) Total biomass of all branches and of the outer-most 2 branch segments at different concentrations of CO₂, and b) total biomass of buds at different concentrations of CO₂.

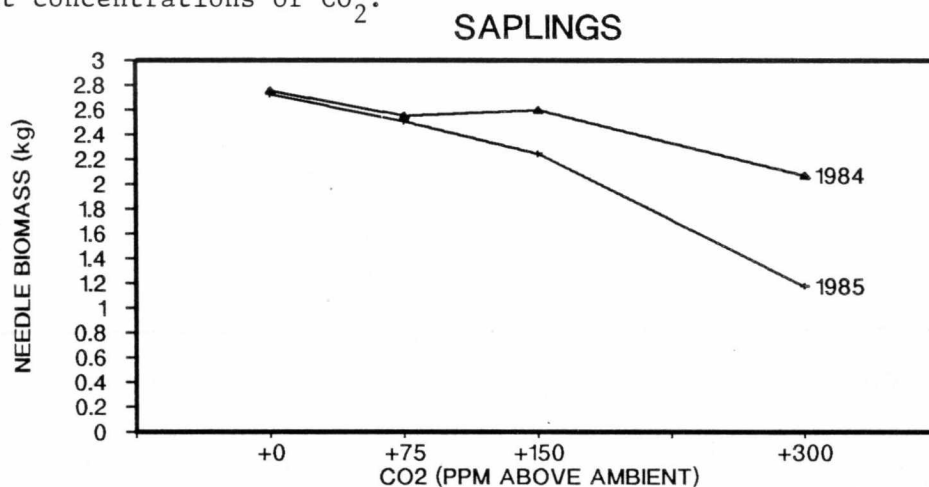


Figure 4. Biomass of two age classes of needles on pine saplings at different concentrations of CO₂.

In a related study (Houpis *et al.*, 1986) the biomass response for seedlings was different in that the greatest production response was observed at +150 ppm with a decline at +300 ppm, though not below the level of the control.

Nutrient Concentrations in Saplings and Seedlings

With the exception of sulfur, none of the nutrients measured was deficient in any of the saplings. When concentrations of N, P, K, S, Ca, Mg, Mn,

Fe and Zn were compared with Weibull probability distributions that have been developed for those nutrients based on samples of ponderosa pine from 78 unfertilized sites on the West Coast where ponderosa pine is native (Zinke and Stangenberger, 1981), the needles from this experiment were found to rank above the 25th percentile for all except sulfur in the sapling needles. The concentration of sulfur in the 1984 sapling needles ranged from 0.04 to 0.07%, or from below the 0th to the 15th percentile, and was lowest at +300 ppm. In contrast, the sulfur concentrations in the 1984 seedling needles were between 0.19 and 0.27 %, well above the 99th percentile.

Concentrations of K in both the saplings and seedlings decreased with increasing CO₂ and in the 1985 seedling needles, this decrease was significant ($p < .05$) (Figure 5). Concentrations of Ca, Mg, and Zn in both age classes of sapling needles increased with CO₂ up to +150 ppm, and then declined at +300 ppm (Figure 6). This pattern closely parallels the trend in distribution of fine and very fine roots under the saplings. In the top 35 cm of soil, densities of roots 0 to 5 mm in diameter were 0.55, 1.36, 1.90 and 0.70 cm root/g soil for the +0, +75, +150 and +300 treatments respectively. Concentrations of N, P, Mn, Fe, Cu, and B did not exhibit any consistent trends in either the saplings or the seedlings and ANOVA revealed few significant ($p < .05$) differences in nutrient concentrations in the seedlings.

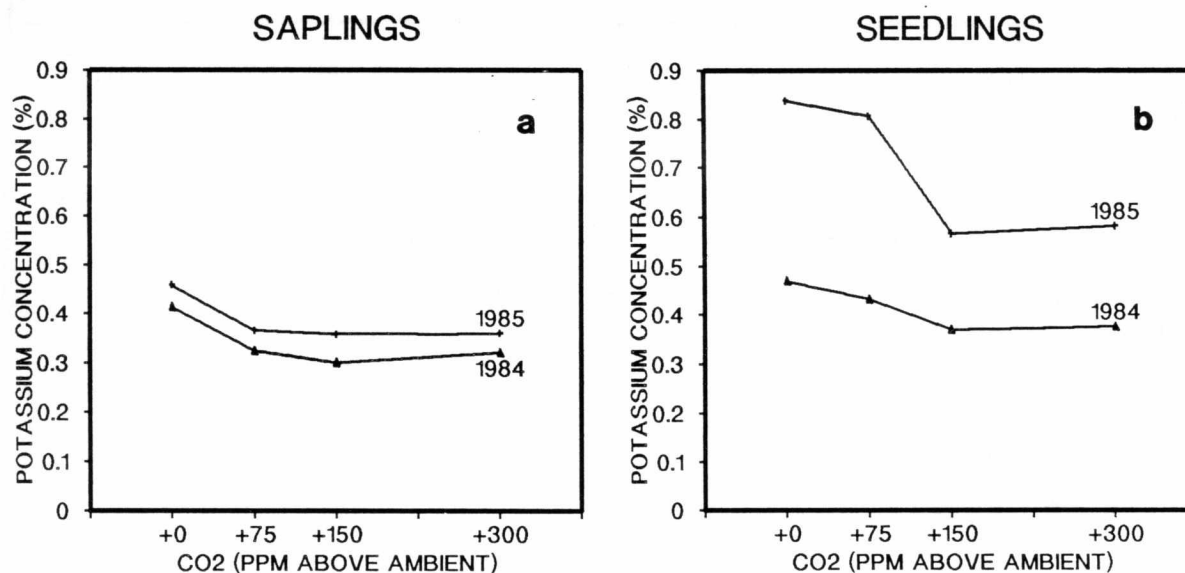


Figure 5. Concentrations of K in two age classes of needles from a) pine saplings and b) pine seedlings grown at different concentrations of CO₂.

DISCUSSION

The changes in stemwood biomass increment indicate that elevated CO₂ may initially favor wood growth; however, this increase does not seem to persist over multiple growing seasons. By the end of the third growing season, wood production of the +300 sapling was considerably reduced below that of the control tree.

The absence of deficiencies in nitrogen and other mobile elements at the higher CO₂ concentrations may be attributable to translocation of these nutrients from the abscising needles on these trees prior to abscission. The

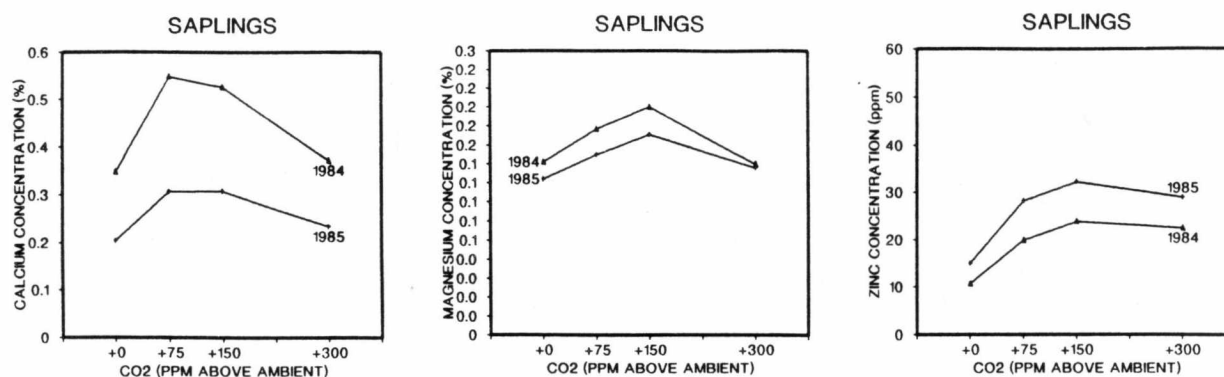


Figure 6. Concentrations of Ca, Mg, and Zn in two age classes of needles from pine saplings grown at different concentrations of CO_2 .

approximate coincidence of the curves relating concentrations of Ca, Mg and Zn and sapling root density to CO_2 concentration could be explained by the trees with larger root systems mining nutrients from a larger soil volume.

CONCLUSIONS

This experiment was part of a preliminary study that was conducted before beginning a much larger, long-term replicated study and was not intended to provide conclusive answers to the questions posed here. Instead, we searched for trends that might warrant further study. The apparent effects on biomass increment and on some nutrient concentrations surely merit further research and a replicated experiment. Future studies on nutrients should assay all plant parts so that a more complete understanding of translocation will be possible. Based on this pilot study, we have no evidence that elevated concentrations of CO_2 are beneficial to ponderosa pine trees over extended periods.

LITERATURE CITED

- Bremner, J.M. 1965. Total nitrogen, Methods of Soil Analysis, Part 2, (Agron. Monogr. 9), Amer. Soc. Agron., Madison, Wisconsin, pp. 1149-1176.
- Echols, R.M. 1970. Moving-slit radiography of wood samples for incremental measurements. In Tree-ring analysis with special reference to Northwest America. J.H.G. Smith and J. Worrall (eds.) Univ. Brit. Col. Fac. For. Bull. No. 7. pp. 34-36.
- Higginbotham, K.O., J.M. Mayo, S. L'Hirondelle, and D.K. Krystofiak. 1985. Physiological ecology of lodgepole pine (Pinus contorta) in an enriched CO_2 environment. Can. J. For. Res. 15:417-421.
- Houpis, J.L.J., K.A. Surano, P.F. Daley and J.H. Shinn. 1986. Growth and morphology of Pinus ponderosa seedlings fumigated for two years with elevated CO_2 . Proceedings of the Ninth N. Amer. For. Bio. Wkshp. Stillwater, OK.

Husch, B., C.I. Miller, T.W. Beers. 1972. Forest Mensuration. John Wiley & Sons, N.Y., p. 122.

Jones, J.B. Jr. 1977. Elemental analysis of soil extracts and plant tissue ash by plasma emission spectroscopy. Commun. in Soil Science and Plant Analysis, 8(4), pp.349-365.

Kimball, B.A., 1983. Carbon Dioxide and agricultural yield: An assemblage and analysis of 430 prior observations. Agron. J. 75:779-788.

Kramer, P.J. 1981. Carbon dioxide concentration, photosynthesis, and dry matter production. BioScience 31:29-33.

Lavender, D.P., and R.B. Walker. 1979. Nitrogen and related elements in nutrition of forest trees. p. 15-22. In J. Murphy (ed.) Proceedings of the Forest Fertilization Conference. Institute of Forest Resources Contribution No. 40. University of Washington, Seattle.

Lemon, E.R. (ed.). 1983. CO₂ and Plants: The response of plants to rising levels of atmospheric carbon dioxide. Amer. Assn. for the Adv. of Sci. Selected Symposium 84. Westview Press, Boulder, CO.

Luxmoore, R.J., E.G. O'Neill, J.M. Ells, and H.H. Rogers. 1986. Nutrient-uptake and growth responses of Virginia Pine to elevated atmospheric CO₂. J. Environ. Qual. (in press).

Rogers, H.H., G.E. Bingham, J.D. Cure, W.W. Heck, A.S. Heagle, D.W. Israel, J.M. Smith, K.A. Surano, and J.F. Thomas. 1980. Responses of vegetation to carbon dioxide: Field Studies of Plant Responses to Elevated Carbon Dioxide Levels. Report 001, U.S. Department of Energy, Carbon Dioxide Research Division, Office of Energy Research, Washington, D.C.

Rogers, H.H., J.F. Thomas, and G.E. Bingham. 1983. Response of agronomic and forest species to elevated CO₂. Science 220:428-429.

Sionit, N., B.R. Strain, H. Hellmers, G.H. Riechers, and C.H. Jaeger. 1985. Long-term CO₂ enrichment affects growth and development of Liquidambar styraciflua and Pinus taeda seedlings. Can. J. For. Res. 15:468-471.

Surano, K.A., P.F. Daley, J.L.J. Houppis, J.H. Shinn, J.A. Helms, R.J. Palassou, M.P. Costella. 1986. Growth and physiological responses of Pinus ponderosa to long-term elevated CO₂ concentrations. Tree Physiology (in press).

Tolley, L.C., and B.R. Strain. 1984. Effects of CO₂ enrichment on growth of Liquidambar styraciflua and Pinus taeda under different irradiance levels. Can. J. For. Res. 14:343-350.

Zinke, P.J., and A.G. Stangenberger. 1981. Ponderosa pine and Douglas-fir foliage analyses arrayed in probability distributions. In S.P. Gessel, R.M. Kenady, and W.A. Atkinson (eds.) Proc., Forest Fertilization Conf. Univ. Wash., Seattle, Coll. Forest Resources, pp. 221-225.

GROWTH AND MORPHOLOGY OF PINUS PONDEROSA SEEDLINGS EXPOSED TO LONG-TERM
ELEVATED ATMOSPHERIC CARBON DIOXIDE CONCENTRATIONS

James L.J. Houpis^{1/}, Kris A. Surano^{2/}, Paul F. Daley^{2/}, and Joseph H. Shinn^{2/}

Abstract.--The growth and morphology of two varieties of Pinus ponderosa were measured after two years of continuous fumigation with carbon dioxide. After two years of treatment, the seedlings of the Rocky Mountain variety showed no significant difference in total stem height or volume, but the basal diameters of those grown at +300ppm CO₂ were significantly greater than those grown at +0ppm and +75ppm. The response of the seedlings of the Sierran variety in these parameters was quite different, with those at +150ppm and +300ppm significantly greater in height than those at +75ppm, and those at +150ppm and +300ppm significantly greater than those at +0ppm and +75ppm in basal diameter and stem volume. However, using a combined analysis based on percent change in height, diameter, or volume, seedlings at +150ppm responded to a significantly greater degree than all other levels. Thus, the beneficial effects of elevated carbon dioxide increase up to +150ppm and begin to decrease between +150ppm and +300ppm.

Additional keywords: Ponderosa pine, Pinus ponderosa var ponderosa, Pinus ponderosa var scopulorum, carbon dioxide, biomass, CO₂ responses.

A long-term fumigation study of the effects of elevated atmospheric carbon dioxide on ponderosa pine (Pinus ponderosa) was conducted at the Lawrence Livermore National Laboratory, Livermore, California. Ponderosa pine was chosen because of its economic importance to the western United States and also because of the scarcity of long-term physiological and morphological studies of the effects of elevated carbon dioxide on long-lived woody species. This paper examines the growth and morphological responses of seedlings in the study. A related study in these proceedings by Fried, et al. (1986) addresses nutrient and biomass responses of saplings.

METHODS

Exposure with elevated carbon dioxide began in July 1983 and was terminated in September 1985. Exposures were continuous and were conducted in four standard open-top fumigation chambers as described by Heagle et al. (1973) and Rogers et al. (1983a, 1983b). The levels of carbon dioxide exposure were ambient (approximately 350ppm; +0ppm), ambient + 75ppm (+75ppm), ambient + 150ppm (+150ppm), and ambient + 300ppm (+300ppm).

^{1/}Department of Forestry and Resource Management, University of California, Room 145 Mulford Hall, Berkeley, California 94720.

^{2/}Environmental Sciences Division, Lawrence Livermore National Laboratory, P. O. Box 5507, Livermore, California 94550.

Work performed under the auspices of the U.S. Department of Energy by the Lawrence Livermore National Laboratory under contract W-7405-ENG-48. Mark P. Costella and Robert J. Palassou are acknowledged for their contribution to this study.

A monitoring system was developed to monitor and maintain these levels (Surano et al. 1986).

The experiments used seedlings of two varieties of ponderosa pine, one being the Sierran variety (*P. ponderosa* var *ponderosa*) and the other the Rocky Mountain variety (*P. ponderosa* var *scopulorum*). At the initiation of the fumigation, the Sierran variety was one-year old, and the Rocky Mountain variety was three-years old. Both varieties of seedlings were potted in 4L containers using a soil mixture containing equal parts of cohasset clay loam, redwood compost, #4 Monterey sand, and perlite. Throughout the study, all seedlings were maintained under well-watered conditions, fertilized regularly, and grown under shade. There were ten seedlings for each treatment.

Growth measurements were taken from April 1984 to August 1985. Basal diameter was determined using a micrometer placed at the cotyledon whorl. Two perpendicular measurements were taken and were averaged. Height measurements were taken from the cotyledon whorl to the top of the apical meristem using a tape measure. Volume was calculated from the diameter and height measurements using a parabolic formula (Husch et al. 1972).

Morphological data were collected at the conclusion of the exposure. Morphological measurements included biomass, volume, specific gravity, height, diameter, needle dry weight and surface area, and the number of buds. Biomass data included dry weight of main stem and lateral stems by age class, roots, needles, and buds. Specific gravity was calculated as the ratio of dry weight per volume of the main stem segment. Height and diameter measurements were taken for each stem segment. Finally, the amount of mid-needle abscission was observed as a percent of total needles present.

Statistical analysis was conducted using analysis of variance, but it

+300ppm respectively. The dry weights per bud for the Rocky Mountain variety were 34, 42, 34, and 72mg for +0ppm, +75ppm, +150ppm, and +300ppm.

Volume

The volumes of the stem segments in the Sierran variety showed similar trends to that of biomass with a statistical grouping of both the two lower and two higher carbon dioxide levels. In the Rocky Mountain variety and in the combined analysis only the volumes of the stem segments at +300ppm were greater than all other treatments. Total volume of the main stem as determined by the the combined analysis is shown in Figure 1.

Analysis of percent change in volume indicated that the higher volume at +300ppm for the Rocky Mountain variety may have been in part due to a statistically larger initial volume. Percent change in volume of the seedlings at +300ppm was only statistically greater than those at +0ppm (rather than +0ppm, +75ppm, and +150ppm as indicated by the ending volume). The percent change in volume for the Sierran variety at +150ppm was greater in percent change than all other treatments, whereas at +300ppm the volume was not statistically different from those at either of the lower carbon dioxide levels (Figure 2). In the combined analysis, the seedlings at +150ppm were also statistically the largest value in percent change in volume (Figure 3).

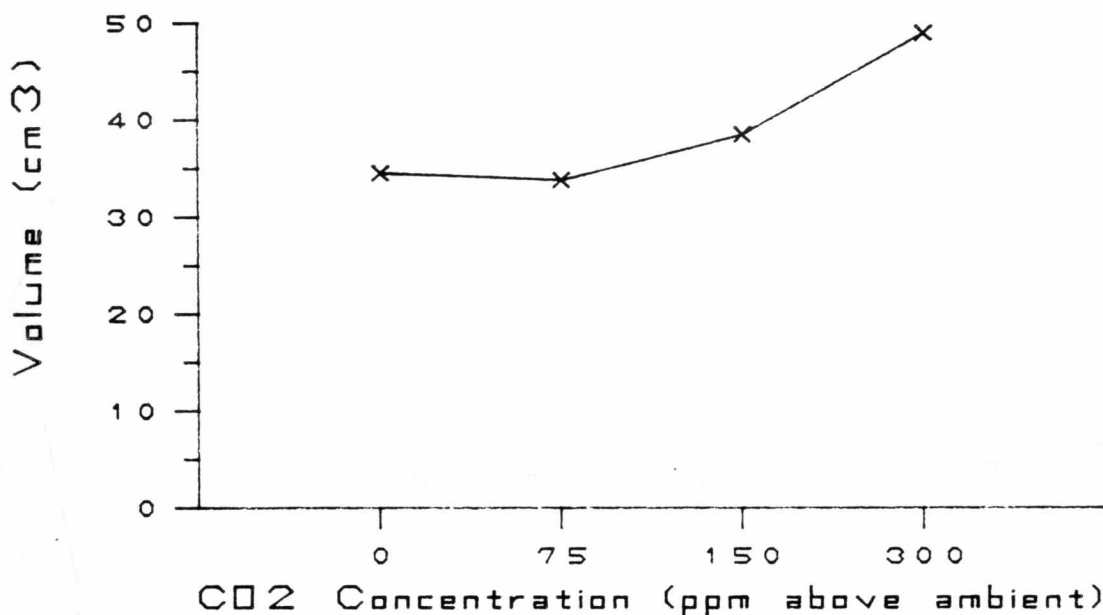


Figure 1.--Volume of the main stem at the various CO₂ treatment levels

Specific Gravity

Specific gravities, using the combined analysis, were 0.485, 0.529, 0.603, and 0.602g/cm³ for +0ppm, +75ppm, +150ppm, and +300ppm treatments respectively. Statistically, only the seedlings at +150ppm and +300ppm were greater than those at +0ppm. The trend observed in specific gravity was due to variations in the Rocky Mountain variety.

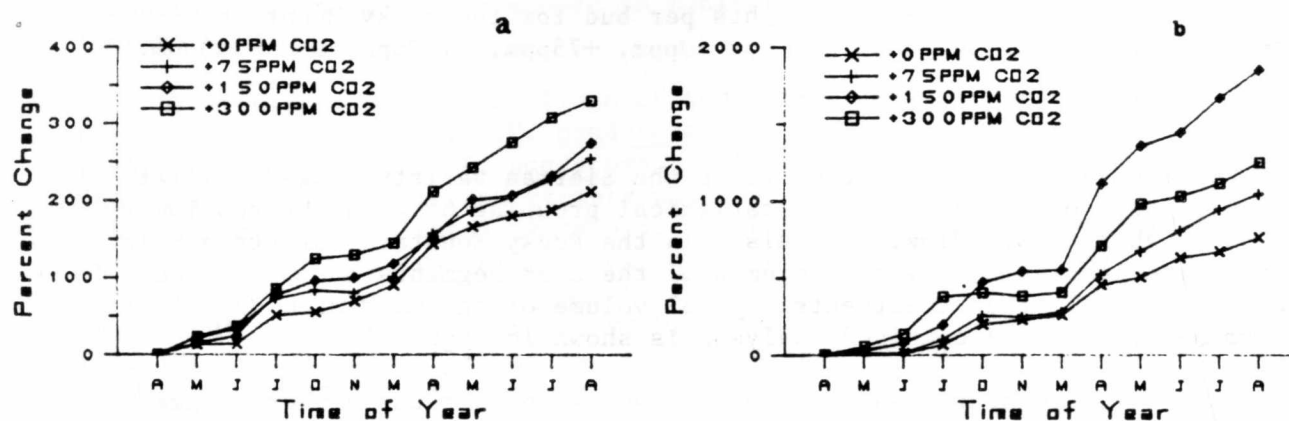


Figure 2.--Percent change in volume over the course of the study for a.) Rocky Mountain, and b.) Sierra.

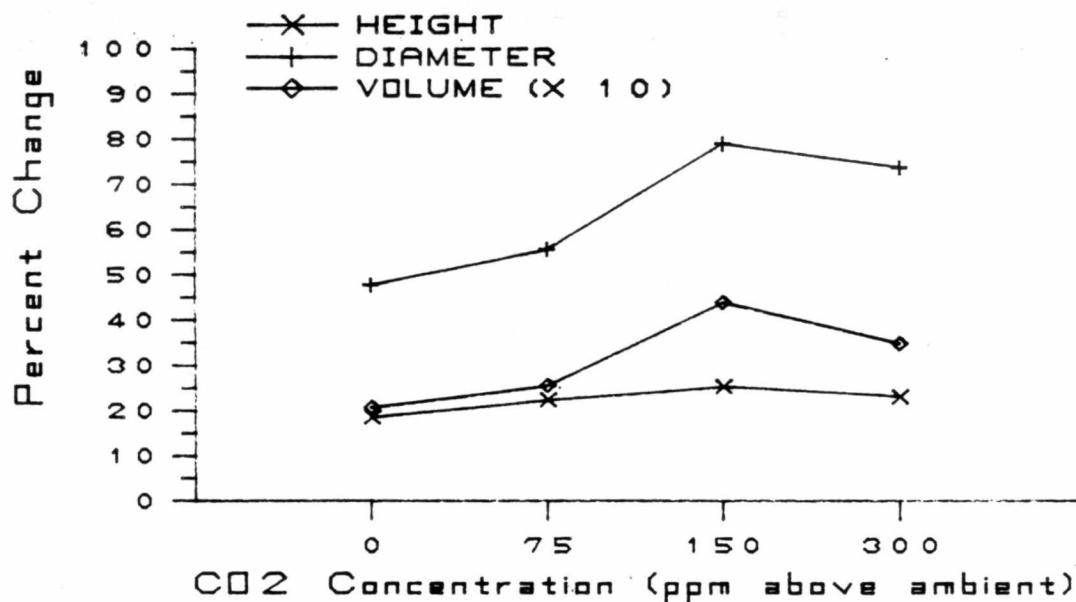


Figure 3.--Percent change in growth of height, diameter, and volume by the end of the experiment using the combined analysis.

Height

At the end of the study, the Sierran variety's seedling heights at +0ppm, +150ppm, and +300ppm were significantly greater than those at +75ppm. This was also true when applying the combined analysis. However, there were no significant differences between any of the treatments for the Rocky Mountain variety (Figure 4).

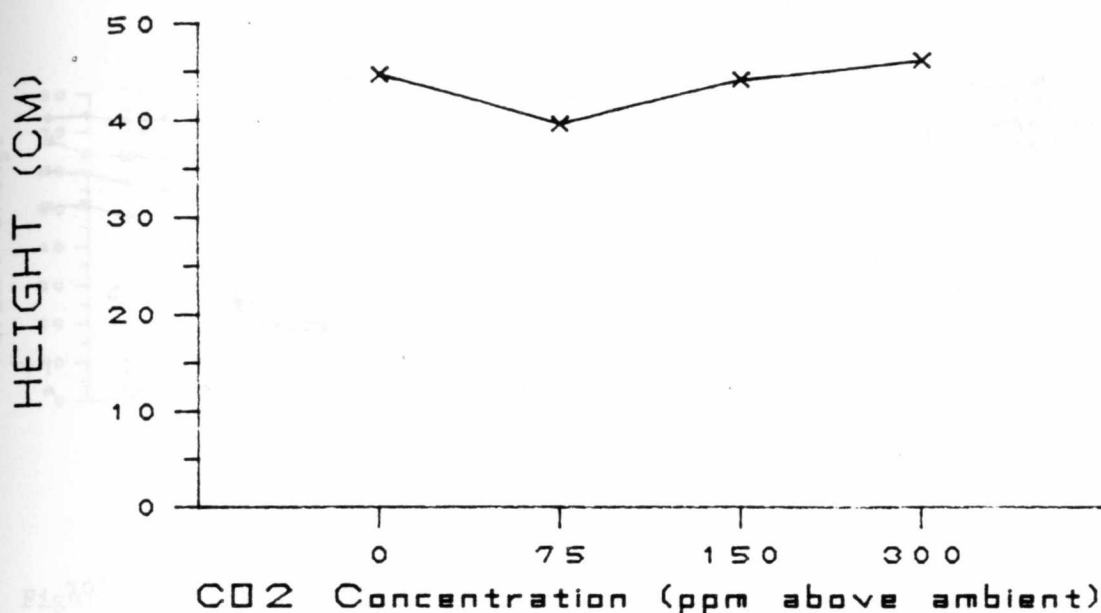


Figure 4.--Height from the cotyledon whorl to the tip of the apical bud for the seedlings in combined analysis.

In the independent analysis of total percent change of height for each variety, only the Sierran variety showed a significant difference (those at +150ppm were greater than those at +0ppm; Figure 5). However, using the combined analysis, the seedling heights at +75ppm, +150ppm, and +300ppm were significantly greater than those at +0ppm, and those at +150ppm were statistically greater than those at +75ppm and +300ppm (Figure 3). Thus, the differences observed in final height in absolute terms and with regard to the seedlings at +75ppm being lowest, can be attributed to a lower initial height.

Diameter

Diameter measurements were taken at each successive whorl up the main stem (Figure 6). In the combined analysis, the basal diameters of the seedlings at +0ppm and those at +75ppm were statistically less than those at +150ppm and +300ppm, and those at +150ppm were less than those at +300ppm. However, when comparing percent change of basal diameter, the seedlings at +150ppm were statistically the largest, followed by those at +300ppm, +75ppm, and +0ppm respectively (Figure 3). One reason for this difference was that the seedlings in the +300ppm treatment had a statistically larger initial basal diameter.

Needle Surface Area

The differences observed in surface area as determined by the combined statistical analysis were due to the Rocky Mountain variety. For the seedlings of the Sierran variety, the only significant difference in total surface area was that those at +300ppm were greater than those at +75ppm, and in the Rocky Mountain variety those at +150ppm were greater than those at +75ppm.

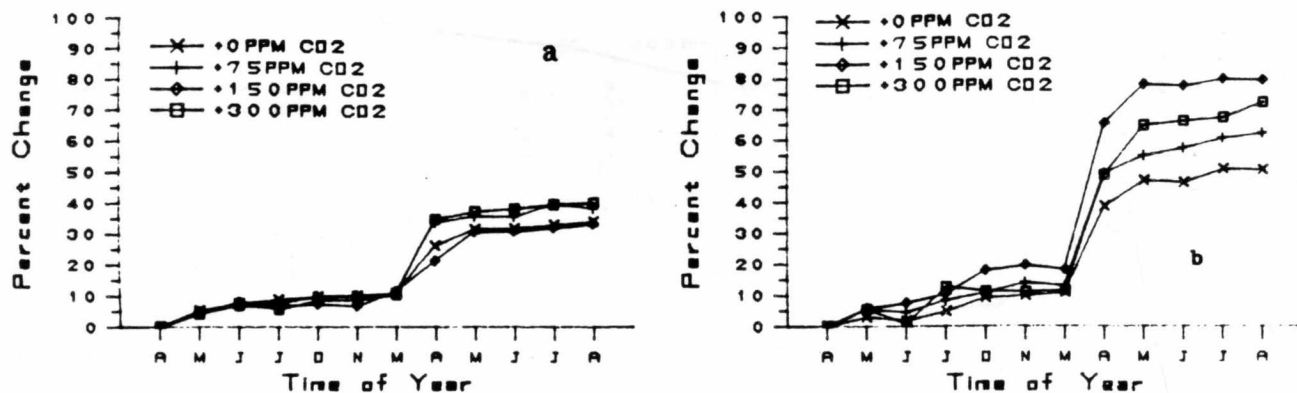


Figure 5.--Percent change in total height over the course of the study for a.) Rocky Mountain, and b.) Sierra.

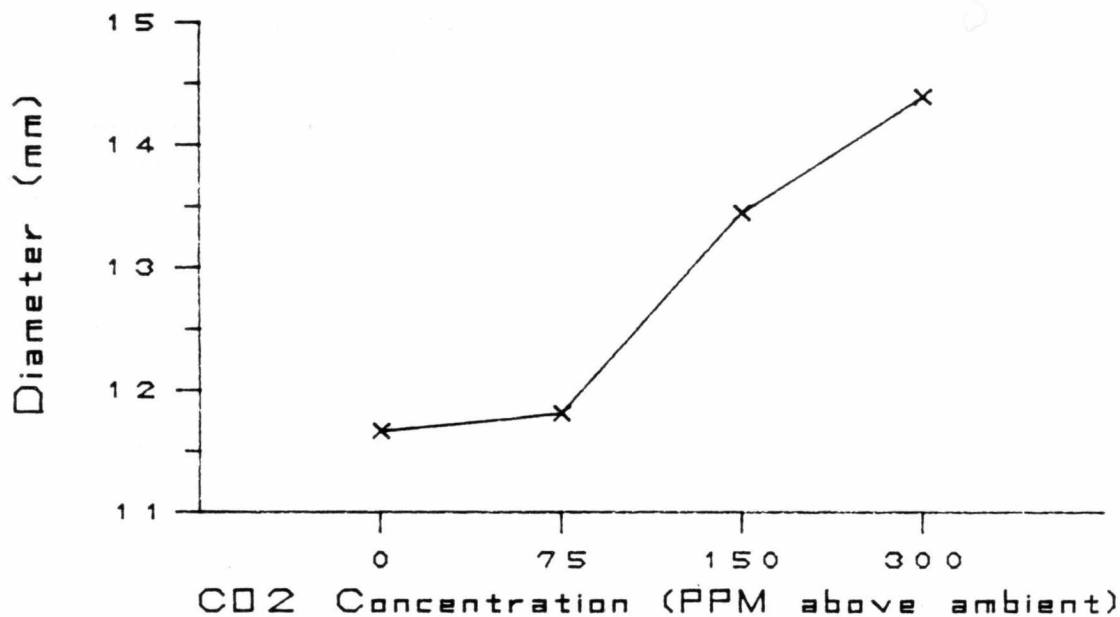


Figure 6.--Stem basal diameter for the combined analysis.

In Table 1 there are indications of a discontinuous phenomenon that occurred between +150ppm and +300ppm with respect to needle surface area. Mid-needle abscission was observed in the +300ppm treatment and this is partially responsible for the high standard deviation and large range for that treatment.

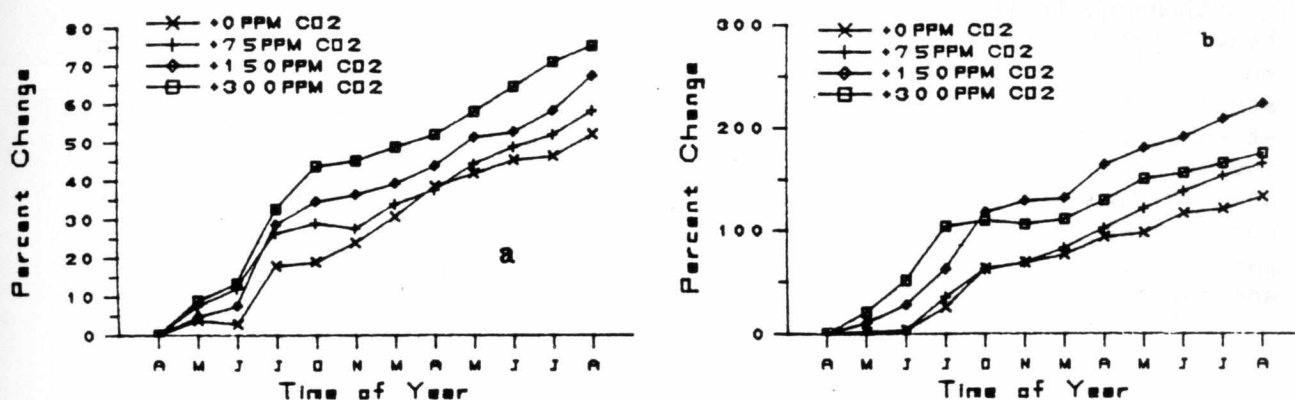


Figure 7.--Percent change in diameter over the course of the study for a.) Rocky Mountain, and b.) Sierra.

Table 1. -- Needle surface area for Sierran variety by carbon dioxide level.

Carbon Dioxide Level (ppm)	Mean	Standard Deviation	Minimum	Maximum
+0	451.83	262.47	142.70	868.67
+75	368.21	236.35	149.20	903.04
+150	592.35	268.21	250.21	1062.71
+300	773.50	587.84	47.57	1924.98

DISCUSSION

Based upon absolute measures of morphology, there was the appearance of a beneficial effect of increasing carbon dioxide. Even though the seedlings were randomized at the start of the study, the seedlings at the +300 treatment were statistically larger in basal diameter and volume. Percent change is a more appropriate measurement because it eliminates the possible bias of initial size. Based upon percent change there were a maximum benefits at +150ppm, with a reduction in growth at +300ppm. This was found in height, volume, and diameter growth. How other factors were affected by initial values, such as biomass and leaf surface area are unknown. Furthermore, the response to elevated carbon dioxide levels appear to be different between varieties of the same species. In particular, at +300ppm the Sierran variety had a reduction in percent growth, whereas the Rocky Mountain variety did not have a corresponding reduction.

CONCLUSION

Although it is generally accepted that increasing carbon dioxide is beneficial to annual plants, it may be premature to extend this conclusion to naturally occurring long-lived plants such as ponderosa pine. This study indicates that there may actually be a detrimental effect beginning at concentrations greater than +150ppm. Such morphological evidence includes a decrease in percent growth and a reduction in needle surface area through mid-needle abscission. This study emphasizes the need for more long-term research on the effects of elevated carbon dioxide, particularly with respect to effects on long-lived woody perennial species and natural ecosystems.

LITERATURE CITED

- Fried, J.S., K.A. Surano, P.F. Daley, J.H. Shinn and P. Anderson. 1986. Biomass production and nutrient responses of ponderosa pine to long-term elevated CO₂ concentrations. Proceedings of the Ninth N. Amer. For. Bio. Wkshp. Stillwater, OK.
- Heagle, A.S., D.E. Body, and W.W. Heck. 1973. An open-top chamber to assess the impact of air pollution on plants. J. Environ. Qual. 2:365-368.
- Husch, B., C.I. Miller, T.M. Beers. 1972. Forest mensuration. John Wiley and Sons, New York, New York, 410pp.
- Neter, J., W. Wasserman. 1974. Applied linear statistical models. Richard D. Irwin, Inc., Homewood, Illinois, 842pp.
- Rogers, H.H., G.E. Bingham, J.D. Cure, J.M. Smith, and K.A. Surano. 1983a. Responses of selected plant species to elevated CO₂ in the field. J. Environ. Qual. 12:569-574.
- Rogers, H.H., W.W. Heck, and A.S. Heagle. 1983b. A field technique for the study of plant responses to elevated carbon dioxide in the field. J. Air Poll. Contr. Assoc. 33:42-44.
- Surano, K.A., P.F. Daley, J.L.J. Houppis, J.H. Shinn, J.A. Helms, R.J. Palassou, and M.P. Costella. 1986. Growth and physiological responses of Pinus ponderosa to long-term elevated CO₂ concentration. Tree Physiology (in press).