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Predicting the effects of tropospheric ozone on regional productivity of ponderosa pine and white fir

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Abstract

We simulated forest dynamics of the regional ponderosa pine–white fir conifer forest of the San Bernadino and Sierra Nevada mountains of California to determine the effects of high ozone concentrations over the next century and to compare the responses to our similar study for loblolly pine forests of the southeast. As in the earlier study, we linked two models, TREGRO and ZELIG, to consider both physiological effects within individual trees and competitive interactions within forest communities. We represented regional effects by simulating at three sites in California, Lassen National Park, Yosemite National Park, and Crestline in the San Bernardino Mountains. At each of these locations, we simulated the response to altered pollutant conditions of 0.5, 1.5, 1.75, and 2 times ambient ozone. Of the two major dominant species in this forest, white fir showed little response, but ponderosa pine was predicted to show large effects. Ambient ozone at Crestline (approximately 110 ppm h, and larger than twice the ambient concentration at either of the other sites) was predicted to decrease individual tree carbon budgets by 10%. This effect was predicted to lead to a decrease in ponderosa pine abundance under average climatic conditions by 16% were these concentrations to continue over the next century. A doubling of ozone at Crestline over the next 100 years was predicted to decrease this budget by an additional 11%, leading to a decline in abundance of 41%. Effects at the other sites were predicted to be smaller (effects of current ambient ozone on abundance of 10% at Yosemite and 0% at Lassen) in proportion to the smaller

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exposures at those sites. Decreases in chronic moisture availability at all three sites were predicted to reduce these effects, particularly if ozone exposures rise.

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1. Introduction

High concentrations of ozone air pollution occur frequently over key forested areas of this country (Takemoto et al., 2001; US EPA, 1996; Miller, 1993). Hourly ozone concentrations at Barton Flats in the San Bernardino Mountains of California were observed to exceed the NAAQS standard of 120 ppb on more than 20% of the sampling days (Watson et al., 1999). Mixed conifer forests in the Sierra Nevada are exposed to 250 ppm h O₃ (cumulative sum of the hourly ozone concentrations) during the growing season (Beyers et al., 1992), and in the San Bernardino Mountains of California season exposures reach 350 ppm h O₃ (Bytnerowicz et al., 1989). Many experimental exposures (Hogsett et al., 1996; Laurence, 1998) and reviews of literature (Chappelka and Samuelson, 1998; McLaughlin and Percy, 1999) have identified the potential for reductions in forest growth from ozone.

Ozone reduces the photosynthetic capacity of large *Pinus ponderosa* (Coyne and Bingham, 1981; Grulke, 1999) and seedlings (Clark et al., 1995), which can lead to reduced carbon gain (Green and Wright, 1977; Weber et al., 1991), reduced biomass (Bytnerowicz and Grulke, 1992; Weber et al., 1994), and alterations in carbon allocation (Hogsett et al., 1989; Grulke et al., 1998; Tingey et al., 1976; Andersen et al., 1991). Trees from heavily polluted areas exhibited reductions in radial growth, missing rings or altered ring formation compared to trees at less polluted sites (Arbaugh et al., 1999; Miller et al., 1997; Miller and McBride, 1998; Miller, 1993).

High ozone levels in the San Bernardino Mountains have been shown to cause damage to individual trees and specific forest stands (Grulke et al., 1998; Miller et al., 1997; Miller and McBride, 1998). O₃ injury to pines has been documented throughout the central Sierra Nevada (Miller and Millecan, 1971; Peterson et al., 1987; Peterson and Arbaugh, 1988; Pedersen, 1989), with amounts of visible injury greater in the

southern than in the central or northern Sierra Nevada (Schilling et al., 1995). Given recent trends in ozone concentrations and the generation of the precursors of ozone in the region, there is no reason to suspect that concentrations will dramatically decrease in the foreseeable future. The goal of this work was to predict effects of ozone that are likely to occur in the future should exposures remain high or increase. We extrapolated individual growth effects on trees to predictions of the alterations in growth that are likely to occur in two major species of trees of a California mixed conifer forest, ponderosa pine (*P. ponderosa* Dougl. ex Laws.) and white fir (*Abies concolor* Gord. & Glend. Lindl. ex Hildebr.), because of exposure to ozone over the next century.

We cannot assume that field observations of past observed effects are indicative of future effects. It is difficult to know the degree to which the specific history of exposure or stand development influenced the effect. Effects of ozone are ideally evaluated by directly fumigating plants, which of necessity are almost always seedlings (Adams et al., 1990; Reich et al., 1987; Temple, 1988; Tseng et al., 1988). These results must be extrapolated to mature tree effects, considering the influences of internal tree processes, which change during tree maturation. Further, interactions among species can significantly alter the effects of ozone (Weinstein et al., 2001). Large trees in competitive environments are unlikely to respond the same way as individual trees in controlled chamber studies. Consequently, this study relied on extrapolating from controlled chamber studies through a series of computer models to determine the susceptibility of forests to ozone damage.

To compare the effects of ozone in different sections of the U.S., we initiated a study that would apply a single methodology to an effort to extrapolate the results from controlled exposure studies to regional impacts in four major forest types, the loblolly pine–yellow poplar forest of the southeast, the ponderosa pine–white fir forests of California,

the oak–maple forests of the mid-east, and the spruce–fir forests of the northeast. Previously, the results from the first of these studies, the regional impact of ozone and precipitation on the growth of loblolly pine (*P. taeda* L.) and yellow poplar (*Liriodendron tulipifera* L.) were reported (Laurence et al., 2001). This paper reports the results from our predictions of the second forest type, ponderosa pine–white fir.

We followed the methodology described in Laurence et al. (2001) in which a combination of two models were used to evaluate how the suppression of the rate of photosynthesis by ozone exposure could cause shifts in individual tree carbon allocation (TREGRO) (Weinstein et al., 1991) and in turn how these shifts could alter the success of the trees in a forest community (ZELIG) (Urban, 1990; Urban et al., 1991). TREGRO has been used previously to assess the consequences of ozone to tree growth in the absence of competition in many different species (Weinstein and Yanai, 1994; Retzlaff et al., 1996; Consable et al., 1996; Consable and Retzlaff, 1997; Weinstein et al., 1998; Laurence et al., 2001). Gap succession models, such as ZELIG, have been commonly used to evaluate the dynamics of natural stand succession (Botkin et al., 1972; Shugart and West, 1977; Shugart, 1984).

We tested whether elevated concentrations of ozone would be sufficient to cause changes in the growth, fine root mass, and leaf mass of individual ponderosa pine and white fir trees at three different locations along the current ozone gradient in the mountains of California in the absence of competition. We then tested whether these predicted changes would be sufficient to alter the competitive dynamics of trees in the ponderosa pine–white fir forests at each of these locations. Our hypothesis was that the changes in forest growth would be proportional to the amount of cumulative ozone exposure at a site, just as tree growth in the absence of competition has been shown to be (Tingey et al., 2001). We expected to predict greater changes in San Bernadino forests, where ozone is already high, than in forests in the central or northern Sierra Nevada Mountains. We further hypothesized that these San Bernadino forests would be more sensitive to increases in ozone than forest further north because of the damage they have already sustained.

2. Methodology

As has been reported in a previous publication describing this methodology (Laurence et al., 2001), we followed eight steps to predict regional effects of ozone on forests.

- (1) We selected climate stations that could be used as a representative section of the climate over which the ponderosa pine–white fir forest is found in California. We used three sites in California, Lassen National Park, Yosemite National Park, and Crestline in the San Bernardino Mountains. From each of these sites, we used the recorded meteorological data (ambient hourly ozone, temperature, precipitation, humidity, and light) from 1990 and 1991, selected because the meteorology and ozone exposure during those years was relatively characteristic of the conditions over the past several decades and because relatively complete data sets were available for all major climatic variables. In all three locations, 1990 had approximately only one-half to two-thirds of the rainfall of 1991. Therefore, we generated a “low or dry” rainfall scenario by using 1990 weather for three successive years, a “high or wet” rainfall scenario by using 1991 for three successive years, and a “medium or normal” scenario by using 1990, 1991, and repeating 1991. We chose this method of creating altered rainfall scenarios in order to maintain the correlation between ozone exposure and temperature and rainfall conditions. Hourly climate data were obtained from the National Oceanic and Atmospheric Administration (NOAA) and hourly ozone data were obtained from the US EPA’s aerometric information retrieval system (AIRS). Thirty-year mean monthly average temperature and precipitation values were obtained from nearby sites in the NOAA database.
- (2) Exposure regimes were created for simulations of the response to 3 years of meteorological data from each of our three sites, Lassen National Park, Yosemite National Park, and Crestline in the San Bernardino Mountains. These exposure regimes included ambient, sub-ambient, and three above-ambient (low, medium, and high) ozone regimes that were generated from hourly ozone monitoring

data at the three climate sites. In the sub-ambient exposure scenario, for days with a maximum 1 h daily concentration > 0.050 ppm, the hourly concentrations were multiplied by the factor 0.05/daily max. Days with daily maximum < 0.050 ppm were not affected.

The above ambient concentrations were generated using these three equations for low, medium, and high scenarios, respectively:

$$\text{Low} = \frac{C_i}{0.60 + 1.2 e^{-50C_i}}$$

$$\text{medium} = \frac{C_i}{0.50 + 1.06 e^{-50C_i}}$$

$$\text{high} = \frac{C_i}{0.46 + 0.7 e^{-50C_i}}$$

where C_i is the ambient concentration for that hour, in ppm.

These sigmoid functions increase monotonically so that the weight increases as ozone concentration increases. These above-ambient profiles are referred to in this paper as 1.5×, 1.75× and 2.00× the ambient ozone, based on maximum daily 1 h concentrations and daily cumulative hour ozone values above 0.060 ppm.

- (3) We established parameters for the TREGRO model to predict expected changes in whole-tree growth, leaf biomass, and fine root mass per unit leaf mass for an average mature tree of each of the two major species of this forest. Parameters used to simulate tree growth with the TREGRO model have been described previously for white fir (Retzlaff et al., 2000) and for ponderosa pine (Consable et al., 1996). Additionally, we assumed that maximum photosynthesis rate will decrease linearly as soil water potential falls below -100 J/kg, ceasing entirely when it falls to -1500 J/kg. Growth of shoots and roots were assumed to decrease linearly as soil water potential goes below -500 J/kg, ceasing entirely when it falls to -10,000 J/kg.
- (4) Ozone uptake was calculated in TREGRO on an hourly basis as a function of stomatal conductance. The maximum potential photosynthesis rate was lowered as a function of the cumulative uptake of ozone in a given leaf class over its lifespan, according to data for ponderosa pine (Coyne and Bingham, 1981, 1982; Weber et al., 1993) and for white fir (Retzlaff et al., 2000).

- (5) Three quantities were predicted with TREGRO, the total carbon gain, the leaf biomass, and the mass of fine root supporting each gram of leaf tissue. The quantities predicted under conditions with altered ozone exposure were compared to those predicted under ambient ozone. In addition, because water availability is known to affect ozone uptake (Tingey and Hogsett, 1985), we predicted these same quantities under conditions in which rainfall was artificially reduced or increased by using the weather from a combination of wet or dry years, as described above in (1).
- (6) A species parameter set for use with ZELIG was constructed for the California mixed-conifer forests containing five species: white fir, incense cedar (*Calocedrus decurrens* Torr.), ponderosa pine, douglas fir (*Pseudotsuga menziesii* Mirb.), and sugar pine (*P. lambertiana* Dougl.). We set the field capacity and wilting point of the soil used in ZELIG based on average soil texture reported for these forests in each of these locations (Jones and Graham, 1993; USDA Forest Service, 1981). ZELIG used the 30-year average and standard deviation of each month's weather to stochastically generate the precipitation and temperature of each month throughout the growing season. Wet and dry scenarios were examined by using the growth changes predicted by TREGRO under a given precipitation scenario instead of explicitly simulating wet or dry weather in ZELIG.

A preliminary simulation of 100 plots, each 600 m² in area, was conducted to generate a stand that could be used as initial conditions for each of the subsequent ozone exposure runs. To establish initial conditions (the collection of trees of various sizes and species) for a mature forest, ZELIG was run under ozone conditions assumed to be in existence during the time the forest was developing. The growth rates of the trees during this development period were adjusted in the ZELIG model until the simulation produced a forest with approximately the same basal area in each of the major species and size distribution as was reported by Miller (1993) from the southern portion of the ponderosa pine–white fir zone. Growth rates of species were adjusted for climatic differences to predict growth at Yosemite and Lassen.

We do not know what the ozone exposure conditions were during this development period, but it is likely that for most of this 100-year period the ozone exposure was below current ambient (or in this case below ambient in 1990–1992) until the last few years. Consequently, the base or control growth rate behavior of the forest predicted with ZELIG was the growth rate expected under sub-ambient conditions, which we assume had a cumulative ozone concentration sum for all hours above 60 ppb (SUM06) equal to zero. Sharp increases in ozone that likely occurred over the last 30 years of this period at Crestline may have made this assumption less reliable at that site. For TREGRO we simulated the growth under different ozone levels directly and did not have to make an assumption about the conditions under which the growth rates were measured.

- (7) The linkage between models consisted of passing three predictions from the TREGRO simulations to the ZELIG model, the total carbon gain, the leaf biomass, and the mass of fine root supporting each gram of leaf tissue. The percent that each white fir and ponderosa pine tree in the ZELIG simulation was modified each year was obtained from the annual average of the ratio of the size of a simulated tree after 3 years of exposure to the

given scenario of ozone compared to the size of a simulated tree under ambient ozone exposure and moisture conditions, as predicted by the TREGRO model. The leaf area of each ponderosa pine or white fir tree was adjusted by the ratio of ozone exposed to unexposed leaf area in the TREGRO simulations. The ratio of fine root mass per unit leaf mass after 3 years of ozone exposure to unexposed was used to proportionately increase the sensitivity of growth to moisture availability directly as the amount of fine root tissue supporting each unit of leaf decreased.

- (8) ZELIG was run for each of the five ozone levels discussed above at each of the three locations, and produced a mean composition for each tree species calculated from the 100 simulated forest plots.

3. Results

3.1. Ozone effects on single tree biomass, leaf biomass, and root to shoot ratio in the absence of competition

In our simulations, the growth of an individual ponderosa pine tree in the absence of competition after 3 years of ozone exposure decreased linearly with the

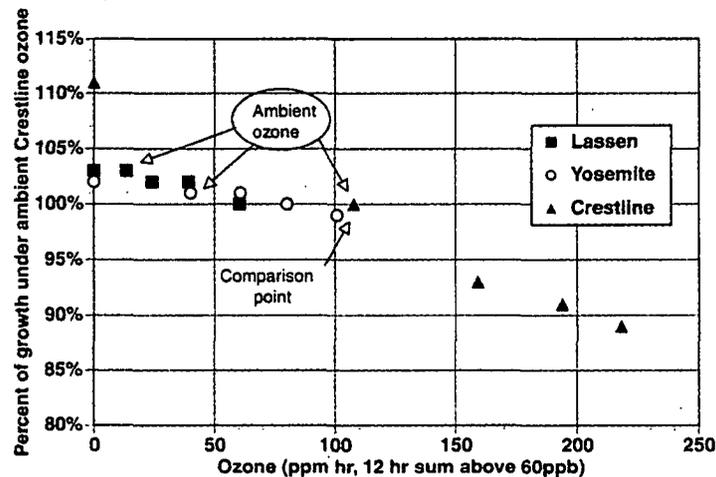


Fig. 1. Effect of ozone on the simulated growth of an individual ponderosa pine tree over 3 years under different levels of ozone. Simulations were conducted at each of three locations, Crestline, Yosemite National Park, and Lassen National Park under ambient rainfall conditions. At each location simulations were run for five ozone levels (0.5 \times , 1.0 \times , 1.5 \times , 1.75 \times , and 2 \times ambient). Ozone is summarized as the cumulative exposure of all hours 8 A.M. to 8 P.M. above 60 ppb over the entire growing season. Ambient ozone at each site is indicated. Growth is shown relative to growth predicted under ambient ozone at Crestline (indicated as "comparison point").

total cumulative exposure of ozone (Fig. 1, Table 1). This figure shows the response of the simulations run for the five levels of ozone at each of the three sites, with each site having a different set of meteorological conditions. Note that the level of ozone exposure under a given scenario was different at the different sites because the scenarios were generated by multiplying ambient concentrations, which were different at different sites. For comparative purposes, the effects of ozone are shown relative to the growth simulated at Crestline under ambient ozone exposure, where growth is reported as 100%. Since individual white fir trees were predicted to be relatively unaffected by all ozone levels, these results are not shown.

The ozone levels are reported as the exposure amount above 60 ppb for any hour from 8 A.M. to 8 P.M.; accumulated through the growing season and summarized in ppm h. Although the model calculates total ozone uptake (cumulative hourly concentrations above zero) and uses this uptake to decrease photosynthesis, we present the results as a function of external exposure of ozone since that quantity is more often reported in comparable literature. The second lowest ozone level in each group of five simulations from a given site was the ambient ozone recorded from that site. One below-ambient and three above-ambient ozone scenarios were run for each site. In all cases, the below-ambient scenarios had an ozone exposure SUM06 of 0. Since Crestline, in the San Bernardino Mountains, currently receives much more ozone than either Yosemite or Lassen National Park, the ambient ozone from Crestline (approximately 110 ppm h) was greater than the highest ozone (twice ambient) used in the simulations at both of the other two sites.

Growth of ponderosa pine trees in the absence of competition appeared to decrease linearly with increases in exposure above ambient across the sites (Fig. 1). Growth was reduced by an approximate average of 0.1% for every 1 ppm h SUM06 of ozone exposure increase. For example, an increase of 110 ppm h SUM06 above ambient levels at Crestline was predicted to produce a reduction in individual tree carbon accumulation of 11%.

Wide differences in site conditions and ambient ozone exposure among the sites caused differences in the rate of decrease in the absence of competition with increasing ozone at different sites (Table 2). Rates of

decline were greatest at Crestline (-0.10% per ppm h SUM06), 50% lower at Lassen (-0.05), and lowest (-0.03) at Yosemite. A reduction of 100 ppm h SUM06 of ozone exposure to a tree growing under ambient moisture conditions at Crestline (comparing ambient to sub-ambient) was predicted to produce an increase in carbon accumulation of approximately 10%, while a similar ozone reduction at Yosemite (comparing the $2\times$ ambient scenario to the sub-ambient) would have been expected to produce only a 4% growth increase.

However, where simulations were run at the different sites under similar exposures, differences in site conditions produced a difference in response of no more than 1%. For example, two simulations, the $1.75\times$ ambient scenario at Lassen and the ambient scenario at Yosemite, had simulations run at 40 ppm h. The effect of an exposure of 40 ppm h under these two different sets of meteorological conditions was similar. Simulations under the $2\times$ ambient scenario at Lassen and the $1.5\times$ ambient scenario at Yosemite, both of which had exposures of 60 ppm h, also produced similar responses. The same was true in a comparison of simulations under the $2\times$ ambient exposure at Yosemite and the ambient exposure at Crestline, both of which had exposures approximately of 100. In all three pairs of cases, the differences in response were within 1%.

At 0 ppm h SUM06 the responses were similar at Lassen and at Yosemite, a 2–3% increase compared to growth at ambient Crestline conditions. However, the simulation at Crestline under 0 ppm h SUM06 indicated that in the absence of significant exposures of ozone under meteorological conditions typical of this site mature ponderosa pine trees would grow 10% faster than they currently do under ambient conditions in the absence of competition.

Changes in ozone did not produce any changes in leaf area. This result was not surprising, since a basic assumption of the TREGRO model is that carbon will be used preferentially to maintain the leaf canopy. However, at all three sites the mass of fine roots available to support each unit of leaf declined dramatically when ozone was increased above $1.5\times$ the site's ambient levels (Fig. 2). The ratio of fine roots to leaf mass is determined by the meteorology and soil conditions at a given site. For example, the ratio at Crestline was 1.02 g fine root per gram of leaf,

Table 1

Percent change in tree mass (TREGRO) or basal area (ZELIG) for white fir and ponderosa pine simulated individually (TREGRO) or in a stand (ZELIG) at three climate stations

Site	Ozone (SUM06)	Precipitation	TREGRO (% change in growth)		ZELIG (% change in abundance)	
			White fir	Ponderosa pine	White fir	Ponderosa pine
Lassen	0	Dry	-0.6	-4.5	-4	-41
	13	Dry	-0.6	-4.6	-4	-21
	24	Dry	-0.6	-4.7	-4	-21
	39	Dry	-0.6	-5.0	-4	-21
	61	Dry	-0.6	-5.7	-11	-19
	0	Normal	0.0	0.2	0	0
	13*	Normal	0.0	0.0	0	0
	24	Normal	0.0	-0.3	0	0
	39	Normal	0.0	-0.8	0	-17
	61	Normal	0.0	-2.3	-5	-26
	0	Wet	0.0	2.9	10	-15
	13	Wet	0.0	2.6	10	-15
	24	Wet	0.0	2.3	13	3
	39	Wet	0.0	1.7	2	-14
	61	Wet	0.0	-0.2	6	-18
Yosemite	0	Dry	0.2	-0.5	-15	-5
	40	Dry	0.2	-1.3	-17	15
	61	Dry	0.2	-2.0	-13	-5
	80	Dry	0.2	-2.8	-14	7
	101	Dry	0.2	-4.2	-11	-6
	0	Normal	0.0	0.8	0	0
	40*	Normal	0.0	0.0	-7	-10
	61	Normal	0.0	-0.7	1	-16
	80	Normal	0.0	-1.8	-4	-13
	101	Normal	0.0	-3.0	-7	-12
	0	Wet	-0.1	1.9	1	-16
	40	Wet	-0.1	1.4	11	-12
	61	Wet	-0.1	1.0	11	-12
	80	Wet	-0.1	0.2	6	-43
	101	Wet	-0.1	-1.2	-3	-27
Crestline	0	Dry	-0.3	9.0	-40	23
	108	Dry	-0.3	-0.1	-37	14
	159	Dry	-0.3	-6.7	-36	2
	194	Dry	-0.3	-9.3	-28	-8
	218	Dry	-0.3	-10.9	-18	-14
	0	Normal	0.0	9.9	0	0
	108*	Normal	0.0	0.0	5	-16
	159	Normal	0.0	-6.7	12	-29
	194	Normal	0.0	-9.3	21	-37
	218	Normal	0.0	-10.9	6	-41
	0	Wet	-0.2	10.9	18	-29
	108	Wet	-0.2	0.0	11	-29
	159	Wet	-0.2	-6.7	18	-33
	194	Wet	-0.2	-9.3	19	-39
	218	Wet	-0.2	-10.9	26	-53

TREGRO values are growth relative to that simulated under ambient precipitation and ozone at each site, and ZELIG values are abundance relative to that simulated under ambient precipitation and 0 SUM06 ozone at each site. Ambient ozone levels are indicated by an “*”.

Table 2

Ozone-induced rate of reductions in growth in ponderosa pine with and without inter-tree competition

	Percent reduction without competition (TREGRO)	Percent reduction with competition (ZELIG)
Crestline	0.10	0.19
Yosemite	0.03	0.12
Lassen	0.05	0.48

The ozone effect is the percentage reduction in the annual biomass increment (TREGRO) or 100-year basal area increment (ZELIG) caused by exposure to ozone compared to the respective increment at 0 SUM06 ppm h, in $\% \times (\text{ppm h})^{-1}$.

whereas at Yosemite it was 0.96 g g^{-1} . The degree to which ozone at a given site altered the characteristic ratio for that site is a measure of the change in the ability of a tree to function optimally at that site. A 10% shift from the characteristic root to leaf ratio at Crestline would be an equivalent impact on the tree to a 10% shift in this ratio at Lassen. At all three sites, doubling the ozone exposure from ambient reduced the fine root to leaf ratio 8% regardless of whether the ambient ozone was already high, as it is at Crestline, or low, in Lassen (Fig. 2).

3.2. Ozone effects on the growth of ponderosa pine and white fir populations in forest stands

We then used the ozone effects predicted for individual trees in the absence of competition from the TREGRO simulations to analyze their consequences in the presence of competition to long-term forest dynamics and development in ponderosa pine–white fir-dominated forest stands, using the ZELIG model. Under ambient moisture conditions in the ZELIG simulations, predicted changes in tree growth and morphology led to large decreases in the basal area of ponderosa pine after 100 years compared to the basal area that would be predicted in the absence of ozone (Fig. 3). Climatic differences among the sites caused predicted abundances of ponderosa pine after 100 simulated years under ambient ozone conditions to be considerably different ($35 \text{ m}^2 \text{ ha}^{-1}$ basal area at Crestline, 16 at Yosemite, and 4 at Lassen). Consequently, Fig. 3 shows the effects of ozone relative to the basal area predicted under 0 SUM06 ozone at each site.

Under the highest ozone scenario at Crestline ($2 \times$ ambient), the ZELIG model predicted a decrease of

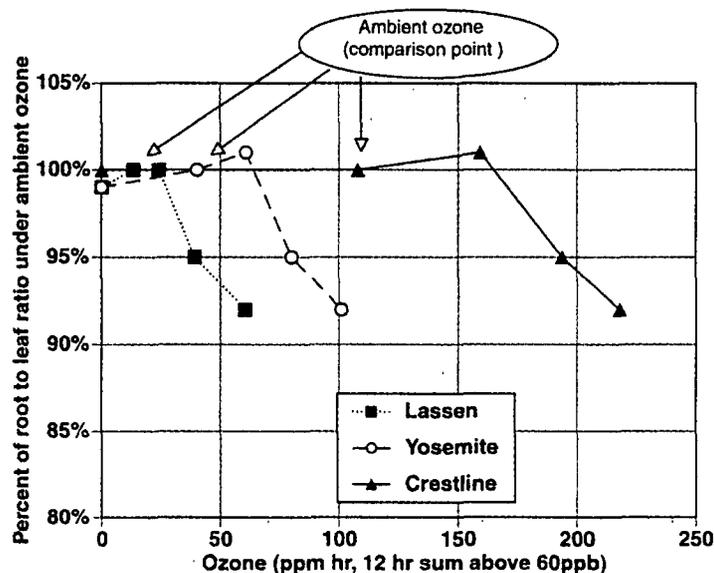


Fig. 2. Effect of ozone on the simulated root to shoot ratio of an individual ponderosa pine tree over 3 years under different levels of ozone. Simulations were conducted at Crestline, Yosemite National Park, and Lassen National Park under ambient rainfall conditions. At each location simulations were run for five ozone levels ($0.5 \times$, $1.0 \times$, $1.5 \times$, $1.75 \times$, and $2 \times$ ambient), under ambient rainfall conditions. Ozone is summarized as the cumulative exposure of all hours 8 A.M. to 8 P.M. above 60 ppb over the entire growing season. Ambient ozone at each site is indicated. Growth is shown relative to growth at each respective site predicted under ambient ozone (indicated as "comparison point").

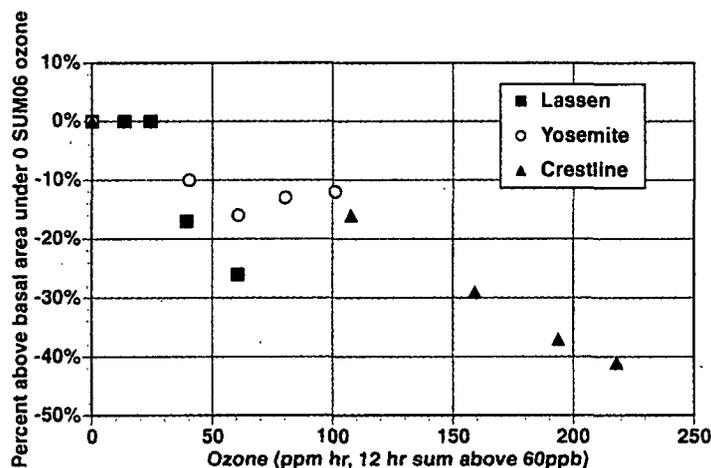


Fig. 3. Simulation of ponderosa pine basal area after 100 years of growth within a ponderosa pine-white fir forest under different ozone exposures at Crestline, Yosemite National Park, and Lassen National Park. Basal area is shown in comparison to basal area grown in the absence of ozone. Ozone is summarized as the cumulative exposure of all hours 8 A.M. to 8 P.M. above 60 ppb over the entire growing season.

41% in the basal area of ponderosa pine compared to what we would have expected at an ozone exposure of 0 SUM06 (Fig. 3, Table 1). Increases in ozone above ambient at all sites were predicted to produce sharp declines in the basal area of ponderosa pine during 100 years of ozone exposure. The ZELIG simulations at Lassen suggested that ponderosa pine basal area would not be affected until the ozone exposure exceeded 30 ppm h. Although there was quite a bit of variability between the responses at Lassen and Yosemite to exposures in the range of 30–80 ppm h, Yosemite and Crestline had similar reductions of 12–16% in response to exposures near 100 ppm h. Yosemite basal area decreased until cumulative ozone exposure was over 60 ppm h; exposures at 80 and 101 ppm h showed no further suppression of the basal area.

The ZELIG simulations suggested that the relatively small ponderosa pine population at Lassen was quite a bit more sensitive to low exposures of ozone. Lassen had the sharpest decline of any site, and the greatest suppression of abundance at ozone exposures of 40 and 60 ppm h. The rate of decrease with increasing ozone at Lassen (-0.48% per ppm h SUM06 over 100 years) was more than twice that at either of the other sites (Table 2). At Yosemite the relative suppression of basal area was approximately half what was simulated at Lassen under similar exposures, and overall the rate of % basal area

decrease there was one-quarter the rate at Lassen. At Crestline the abundance was intermediately sensitive to ozone in the presence of inter-tree competition, unlike the response of growth to ozone in the absence of competition, where the Crestline simulations were the most sensitive.

At both Lassen and Yosemite, large decreases in ponderosa pine at the higher ozone exposures did not result in large changes in white fir abundance (Fig. 4). Such changes might have been expected since ponderosa pine and white fir compete directly for resources within the forest, so that gains by one species reduce the resources available to the other. In fact, white fir basal area declined at both these sites under the highest ozone. Given the insensitivity of individual white fir trees to ozone in the absence of competition, it would be expected that this species might take advantage of decreases in the ponderosa pine population. However, the ZELIG simulations suggested that a diversity of species other than white fir would take advantage of the opportunities in increased resource availability under moderate ozone exposure. In simulations of the response to the highest ozone levels at the Crestline site, the suppression of ponderosa pine basal area was so large that white fir did respond to the decrease in competition from pine and showed increases of up to 20% in basal area.

The response of ponderosa pine to ozone depended on the available moisture. In simulations in which annual

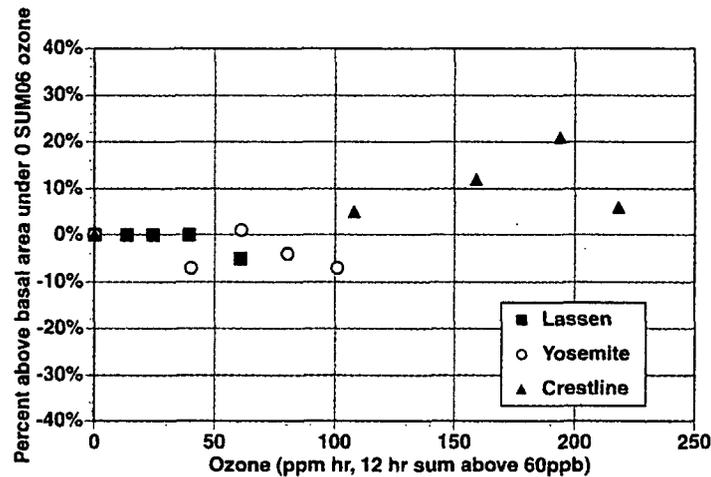


Fig. 4. Simulation of white fir basal area after 100 years of growth within a ponderosa pine–white fir forest under different ozone exposures at Crestline, Yosemite National Park, and Lassen National Park. Basal area is shown in comparison to basal area grown in the absence of ozone. Ozone is summarized as the cumulative exposure of all hours 8 A.M. to 8 P.M. above 60 ppb over the entire growing season.

rainfall was approximately 50% lower, high ozone caused basal area decreases at the Crestline site only (Fig. 5). The negative effects of ozone exposures below 100 ppm h simulated under normal moisture conditions did not occur in these low moisture simulations. Under the highest exposure (218 ppm h), the dry moisture conditions reduced the negative effect of ozone on ponderosa pine basal area from -41% predicted under normal moisture conditions to -14% .

4. Discussion

These simulations indicated that ambient ozone conditions had caused a 10% reduction in growth in the absence of competition at Crestline, and a 1 and 0% reduction at Yosemite, and Lassen, respectively. We predicted that if ozone were to reach twice the ambient levels currently experienced at Crestline (which would then have an ozone exposure of

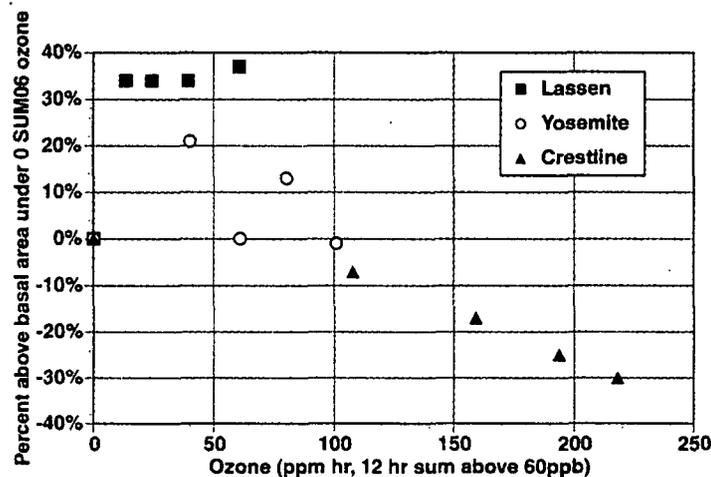


Fig. 5. Simulation of ponderosa pine basal area after 100 years of growth within a ponderosa pine–white fir forest under different ozone exposures at Crestline, Yosemite National Park, and Lassen National Park under low moisture conditions. Basal area is shown in comparison to basal area grown in the absence of ozone. Ozone is summarized as the cumulative exposure of all hours 8 A.M. to 8 P.M. above 60 ppb over the entire growing season.

approximately 220 ppm h, well within the range historically reported from areas of the San Bernardino mountains) the growth rate of mature ponderosa pine trees in the absence of competition would decrease by approximately an additional 11%. Although conditions would have to change considerably at either Yosemite or Lassen for ozone to reach the levels at Crestline, these results suggested that in the absence of competition high levels of exposure would reduce growth to a similar degree.

Both this study and that of Tingey et al. (2001), using the same TREGRO model for similar sites, found effects were less in sites farther north. In addition, both studies identified Crestline as the most sensitive and Yosemite as the least. The magnitude of the responses reported by Tingey et al. (2001) appear different, but the difference may have been caused by the use of a different metric to summarize ozone exposure and because the TREGRO simulations were run for 1 year instead of our 3-year period. Tingey et al. (2001) predicted that 1990 ambient ozone conditions had caused a 47, 5, and 2.5% reduction in growth in the absence of competition in Crestline, Yosemite, and Lassen, respectively, much larger decreases than the predictions of our study. Further, Tingey et al. (2001) simulated much higher rates of decline, with the rates at Yosemite (0.09% decrease in growth per $\mu\text{mol h/mol}$) 40% of those at Lassen (0.15%), and Crestline being 3 \times as sensitive (approximately 0.45%) as Yosemite. The rates simulated in our study were 0.03% per ppm h SUM06 for Yosemite, 0.05% for Lassen, and 0.10% for Crestline. Although the general conclusions of the two studies support one another, the differences in the predicted magnitude of the effects identify the sensitivity of the simulations to the specific meteorology being used to drive the models. Since these two studies used different meteorology, their relative results give some indication of the potential variation in the predicted effects and the degree to which these predictions might be expected to vary with the pattern of future meteorology and ozone conditions.

Our predictions for growth reductions in the absence of competition were much more similar to those of Tingey et al. (2001) than to those of Consable et al. (1996), who reported that a W126 ozone exposure index of $62 \mu\text{mol h mol}^{-1}$ reduced growth by 19%, a rate of 0.3% per unit ozone. Our prediction

Table 3

Simulated carbon budgets (kg/year) for single mature ponderosa pine trees at different locations under 1990 climate

	Crestline	Yosemite
Source	83.7	58.2
Sink	81.1	54.0
Surplus	2.6	4.2

Source is the gross cumulative carbon fixed through photosynthesis plus the carbon remobilized during the year from internal pools. Sink is the cumulative carbon utilized in respiration and construction of new tissue during the year. Surplus is the difference between source and sink.

that growth should decrease linearly with increasing exposure is consistent with the observations of Pedersen et al. (1991) and Arbaugh et al. (1998), both of whom found more injury to trees in the southern mountains of California than in northern California.

Tingey et al. (2001) concluded that ozone sensitivity of trees in the absence of competition increased with increasing precipitation and, to some degree, with decreasing temperature. The most sensitive site in our study was likewise the coolest, but the trend was not consistent. In addition, where simulations were run at the different sites under similar exposures, differences in site conditions produced a difference in response of no more than 1%, suggesting that meteorological conditions among the sites might not influence the ozone response in the absence of competition as much as indicated by Tingey et al. (2001).

Cooler temperatures in the more northerly climate of Yosemite resulted in much less source carbon for ponderosa pine compared to Crestline, using calculated carbon budgets for 1990 as a representative year (Table 3). We expected a tree growing under cooler temperatures to have less surplus carbon available for reallocation and repair, and therefore to be much more sensitive to a decrease in carbon fixation rate. However, because sink demands for carbon were lower, a tree at Yosemite was predicted to have more surplus carbon (4.2 kg versus 2.6 kg at Crestline). This carbon gave the tree more buffer against an ozone-induced reduction in source at Yosemite before demand could no longer be met, making it less sensitive.

When we used our TREGRO predictions of the effect of ozone on tree growth in the absence of

competition in the ZELIG model, we predicted that these changes in growth would lead to large changes in abundance of ponderosa pine in the presence of inter-tree competition. At Crestline, a decrease of 0.1% per 1 ppm h SUM06 in growth caused a decline in ponderosa pine abundance of nearly 0.2% per 1 ppm h SUM06 over the next 100 years. The amplification of response was even greater at Yosemite (4 times) and Lassen (nearly 10 times). The comparison of the rate of decline of annual growth potential in the absence of competition to the rate of decline in species abundance over a 100-year period is somewhat arbitrary, but it is clear that small changes on one scale could become large ones on another.

With more source carbon available for growth under warmer temperatures (Table 3), ponderosa pine trees had a higher growth rate at Crestline than at Yosemite and Lassen, making these trees at Crestline much better competitors than white fir in the corresponding ZELIG simulations. With less source carbon at Yosemite, ponderosa pine had a growth rate there that was much more similar to white fir than it had been at Crestline, making it a weaker competitor against white fir. Although the carbon surplus was greater at Yosemite, increases in ozone depleted this surplus in both locations. Because competition with white fir was already more intense at Yosemite, similar ozone-induced reductions in fixed carbon caused a greater competitive disadvantage to ponderosa pine at Yosemite.

Moisture stress altered these responses. Since both these species are somewhat sensitive to water availability, we expected that simulated trees growing under dry conditions would fix less carbon over the course of the growing season as insufficient moisture limited photosynthesis. If moisture deficit reduced the total fixation of carbon without proportionately reducing demand, the tree would have less surplus carbon and therefore be more sensitive to ozone-induced carbon fixation reductions.

For example, we assumed that the greater evaporative demand at Crestline caused moisture to be more limited than at the other sites, and this limitation, in addition to a greater respiration induced by higher temperatures, led to the small carbon surplus (Table 3). We expected that plants already in a state of carbon shortage would be more sensitive to any further reduction in available carbon induced by ozone

exposure. Consequently, we expected trees there would be the most sensitive to ozone. Further, we expected that when we reduced moisture availability at this site the sensitivity of population abundance to ozone would be further increased. However, while the simulated ponderosa pine trees at Crestline were the most sensitive to ozone in the absence of competition, they were able to maintain their basal area in the forest in the presence of high ozone more effectively when moisture was low than when moisture availability was high.

Moisture deficit made ponderosa pine abundance at all three sites less susceptible to injury under a given level of ozone exposure. Negative responses in ponderosa pine abundance at Yosemite and Lassen did not occur under reduced moisture availability, and the abundance at Crestline was decreased by 25%. In fact, at both Yosemite and Lassen, ozone caused abundance to increase under conditions of reduced available moisture.

Other studies (Temple et al., 1992; Temple and Miller, 1996) have shown that if moisture deficit is sufficient to decrease conductance and the uptake of ozone, the effects of ozone on photosynthesis will be proportionately decreased. In our study, reducing available water by approximately 50% could have directly reduced the stomatal conductance during periods of the growing season by 30–50%, which in turn could have reduced cumulative ozone uptake by an equivalent amount. Since the effect of ozone was directly proportional to uptake, moisture stress could have led to a decrease in the influence of ozone. Trees were predicted to benefit more from the reduction in cumulative ozone uptake caused by the effect of moisture stress on stomatal opening than they lost from the reductions in gross photosynthesis that moisture stress also caused.

In addition, it is conceivable that ozone caused an extension of the growing season through its effect on decreasing photosynthesis and, in turn, stomatal conductance. Trees exposed to ozone may have had less conductance early in the growing season, leaving more water available later in the season. As a consequence, despite the reduction in photosynthetic rate experienced by the ozone-exposed trees, they could have achieved a greater productivity because they were able to conduct photosynthesis much longer into the dry season, when normally trees had shut

down photosynthesis because of dry soil conditions. We were not able to determine whether this phenomenon was causing the response observed in this study.

Any growth increases under reduced moisture conditions were quite surprising given that ozone caused reductions in the amount of root material available to support each unit of leaf at all of the sites (Fig. 2). Ponderosa pine trees should have been more sensitive to moisture stress under high levels of ozone in the ZELIG simulations. However, the increase in moisture sensitivity did not greatly alter the predicted performance of trees in the forest community. The reduction of the effect of ozone on growth rate caused by moisture deficit-induced decreases in ozone uptake proved to be much more important, decreasing the impact of ozone on basal area of pine.

The magnitude of the responses predicted for ponderosa pine in this study was similar to that predicted for loblolly pine and yellow poplar in the southeastern US in the previously reported portion of this analysis (Laurence et al., 2001). In the absence of competition, ponderosa pine was more sensitive to ozone than either of the species in that earlier work, and white fir was less sensitive. For example, at an ozone exposure of approximately 200 ppm h, loblolly pine growth was changed approximately -0.5 to -1.5% and yellow poplar from -0.5 to -2.5% , depending on site and moisture (Laurence et al., 2001, Tables 1 and 3), while ponderosa pine in our study was predicted to change -9.3% and white fir -0.5% . Although it is somewhat difficult to use controlled chamber responses from experiments conducted under different meteorological conditions, the order of sensitivity among these species in the absence of competition was generally as expected (Coyne and Bingham, 1981, 1982; Sasek et al., 1991; Cannon et al., 1993; Weber et al., 1993; Retzlaff et al., 2000).

Once competition was considered, however, Laurence et al. (2001) predicted that shifts in species abundance were similar in magnitude. Loblolly pine growth was predicted to decrease up to 9% and yellow poplar to 34%, while ponderosa pine was predicted to decrease 41% and white fir increase 6% under equivalent high ozone concentrations. Predicted changes in the basal area of loblolly pine over the 100-year period ranged from an increase of 44% to a decrease of 43%, and in yellow poplar from 36% to

-23% in their study, depending on location, ozone, and precipitation. In this study, ponderosa pine responses ranged from 23% to -53% and white fir from 26% to -40% . Despite these large ranges of response, we find a similar conclusion as Laurence et al. (2001) that large changes are not predicted for this forest over its range unless current ozone levels increase dramatically. However, both studies identified specific local sets of conditions that are predicted to lead to large changes in species abundance.

If these simulations mirror the real system, individual trees are capable of buffering the effects of photosynthesis reductions, relying on mechanisms that permit growth to occur at rates greater than would have been expected given the reductions of available carbon from reduced photosynthesis. However, the simulated reductions in growth in individual trees were magnified at the stand level, where inter-tree competition occurred. The exposure experiment of Coyne and Bingham (1981, 1982) indicated that a cumulative exposure reaching 200 ppm h by the end of the growing season would decrease photosynthesis 85%, leaving the rate only 15% of what it would have been without ozone effects (Fig. 6). In our simulations using this photosynthesis response, this reduction in photosynthesis caused the growth of an individual tree in the absence of competition to decrease only an annual average of 21%, not 85%.

Our preconceived notion is that a response at one scale should translate directly to another scale. Consequently, when we take an experimental result such as an 85% decrease in photosynthesis, we assume this must lead to a similar decrease in individual tree growth in the absence of competition. Further, an 85% decrease in each tree's tree growth might be expected to cause a loss of population biomass of about the same magnitude. However, the TREGRO model estimates the amount that an individual tree's growth is buffered against a loss of growth despite a decline in photosynthesis. For a short time period at least, a tree has reserves that can be tapped to meet the demand for growth when photosynthesis is in short supply. Typically, there is variation in the severity of ozone exposures from year to year, so that trees experience a respite during which these reserves can be replenished. If every year was a severe ozone year, we might expect that eventually the buffers would be depleted and tree growth would sink to the level of

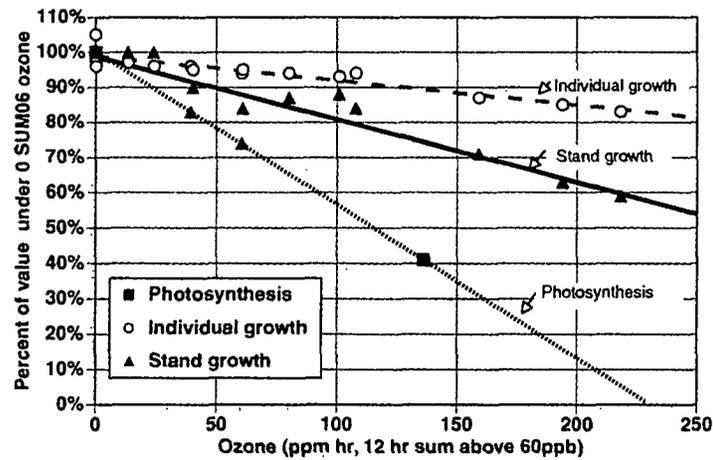


Fig. 6. Comparison of the simulated effect of ozone on ponderosa pine at three different scales of biological organization. Points represent predictions made by TREGRO ("individual growth") and by ZELIG ("stand growth") in this study. Photosynthesis effect was reported by Coyne and Bingham (1981).

photosynthesis reduction. However, it is more common to see tree growth diminish more gradually than would be indicated from the direct effect of stress on photosynthesis.

However, a 200 ppm h cumulative exposure of ozone in the presence of competition was predicted to reduce the basal area of the species by 35%, a larger value than would have been expected from the growth reductions in the absence of competition. Unlike the

integrated processes within a single tree that can partially compensate for injury, competition among individuals at the stand community level accentuated the effects on any one tree. A tree that grows slower in height because of exposure to ozone can readily find other trees over-topping it and loses a proportional amount of access to the light available in the canopy because the neighboring trees are growing relatively faster. Since volume accumulation tends to be directly

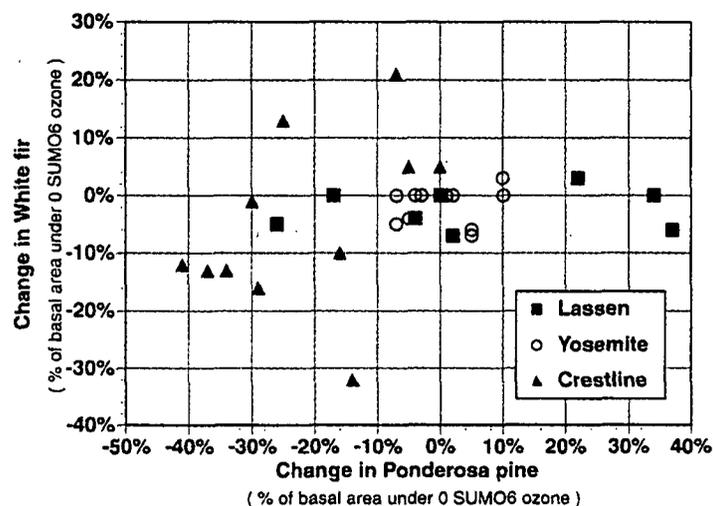


Fig. 7. Simulated change in white fir basal area after 100 years predicted in simulations of three different precipitation regimes on each of the three sites compared to the change in ponderosa pine predicted for that same site under the same moisture.

related to the amount of light intercepted (Shugart, 1998) and light decreases exponentially down through the forest canopy (Waring and Running, 1998), trees whose growth has slowed and consequently have their leaf area lower in the canopy experience decreases more rapidly that would be expected from the decrease in tree growth. Over time the direct effect of ozone is magnified by its indirect effect on decreasing the ability of the tree to gain access to needed resources.

It was expected that any reduction of growth of one principal species in the forest would cause a proportional increase growth in its major competitor as light and water became more abundant. However, we did not see a direct correlation among the responses of ponderosa pine and white fir under the same ozone and climate conditions (Fig. 7). This lack of correlation does not necessarily mean that ozone did not alter the ability of species to compete. It is conceivable that the growth reductions caused by ozone exposure were sufficient to prevent ponderosa pine trees in the simulations from over-topping white fir trees, dramatically reducing their access to light. White fir trees are relatively insensitive to changes in light environment and are incapable of accelerating growth dramatically. Therefore, it is possible to imagine competition playing a major role in accentuating the effect of ozone on ponderosa pine without white fir showing a concomitant increase.

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or commercial products constitute endorsement or recommendation for use.

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