ELEVATED CO_2 AND TEMPERATURE ALTER THE RESPONSE OF *PINUS PONDEROSA* TO OZONE: A SIMULATION ANALYSIS

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Abstract. We investigated the potential impact of projected future temperature and CO_2 concentrations in combination with tropospheric O_3 on the annual biomass increment of *Pinus ponderosa* Doug. ex Laws. TREGRO, a process-based whole-tree growth model in which trees experienced a seasonal drought, was used to study the interactions of CO_2, temperature, and O_3 on tree growth along a latitudinal gradient in California, Oregon, and Washington, USA. The annual biomass increment increased in proportion to CO_2 concentration, although the magnitude varied among sites. Increasing air temperature (+1.3°C) increased growth at most sites. Elevated CO_2 increased the temperature optimum for growth at four sites and decreased it at two sites. The annual biomass increment decreased with increasing O_3 exposure. The differences in O_3 effects among sites were primarily controlled by differences in precipitation. Although increasing CO_2 can reduce the O_3 impact, it does not eliminate the impact of O_3. Elevated CO_2 would enhance tree growth more if O_3 exposures were reduced, especially in the more polluted sites. The greatest benefit for tree growth would come from reducing O_3 exposures in the most polluted sites, but we must also consider locations that have high inherent O_3 sensitivity because of their mesic conditions. Limiting the increase of O_3 levels in those areas will also increase tree growth.

Key words: drought stress; elevated CO_2; ozone, tropospheric; Pinus ponderosa; *temperature; TREGRO.*

INTRODUCTION

Tropospheric O_3 is recognized for its unique phytotoxic properties (U.S. EPA 1998). Its regional distribution patterns make it likely to influence the structure and productivity of forest ecosystems throughout the U.S. and other industrialized countries. Effects on forest ecosystems are likely to increase in areal extent as more countries, particularly developing ones, become more industrialized or agriculture more managed (Chameides et al. 1994).

Needle injury and loss were first observed on *Pinus ponderosa* Doug. ex Laws in the early 1960s in the San Bernardino Mountains, of California, USA, and attributed to O_3 exposure (Miller and McBride 1999). Subsequent studies confirmed that *P. ponderosa* is among the forest tree species most susceptible to O_3 (Miller et al. 1989). Using a range of sites throughout the San Bernardino and Sierra Nevada Mountains of California, USA, Arbaugh et al. (1998) established that foliar injury was highly correlated with the ambient O_3 exposure. Ozone reduces the photosynthetic capacity of large *P. ponderosa* (Coyne and Bingham 1981, Grulke 1999) and seedlings (Clark et al. 1995). Stomatal conductance decreases with increasing O_3 exposure and

normal stomatal function is lost (Grulke 1999). Ozone exposure causes premature needle loss, which contributes significantly to the reduced carbon gain (Green and Wright 1977, Weber et al. 1991) and reduced biomass (Bytnerowicz and Grulke 1992, Weber et al. 1994). Ozone alters carbon allocation as evidenced by alterations in biomass partitioning (Hogsett et al. 1989), reduced root biomass (Grulke et al. 1998), and reduced starch storage in roots (Tingey et al. 1976, Andersen et al. 1991). It is suggested that the combination of drought and O_3 exposure reduced the radial growth of *P. ponderosa* and *P. jeffreyi* in the San Bernardino Mountains by 25–45% over the period 1950 to 1975 (Arbaugh et al. 1999). The O_3-induced reduction in carbon assimilation and altered allocation renders the trees more sensitive to competition and insect infestation and is a contributing factor to the increased tree mortality observed in the San Bernardino Mountains (Arbaugh et al. 1999).

Few studies, however, have investigated the combined effects of O_3 and changed air temperature and atmospheric CO_2 concentrations on forest tree species. Allen (1990) suggested that reduced stomatal conductance from elevated CO_2 could potentially reduce the damaging effects of ambient O_3. Several studies have examined the effects of increased CO_2 and O_3 on photosynthesis, growth, and carbon partitioning in *Acer saccharum* Marsh. (Nobel et al. 1992), seedlings of
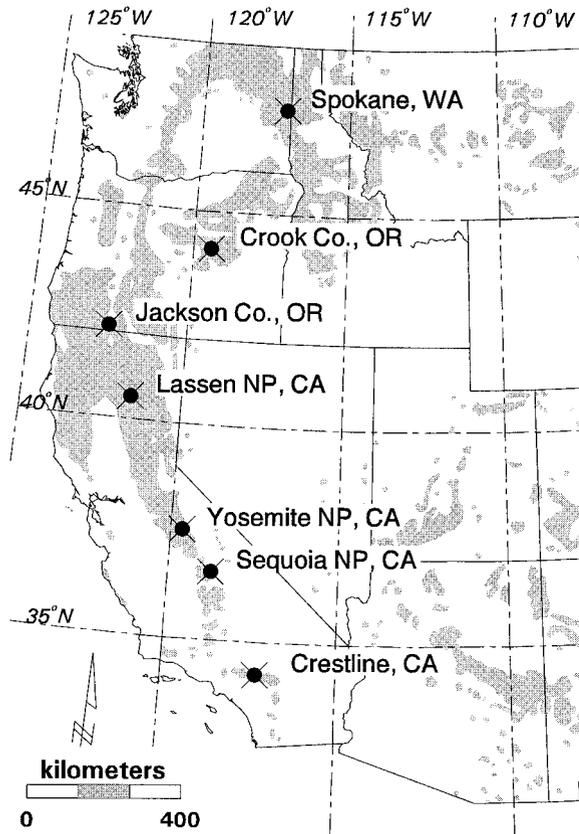
FIG. 1. Ponderosa pine distribution was derived from a map prepared by Little (1971). State abbreviations: CA, California; OR, Oregon; WA, Washington.

nine conifers (Mortensen 1994), *Betula pubescens* Ehrh. (Mortensen 1995), and *Pinus sylvestris* L. (Kellomäki and Wang 1997). Although there is some variation among species, these studies suggest that the increased plant growth from elevated CO$_2$ may be reduced by increasing tropospheric O$_3$. Using a simulation model, Constable et al. (1996) reported that elevated CO$_2$ reduced the impact of O$_3$ on *P. ponderosa* while increasing temperature increased the O$_3$ impact. However, in their simulation study soil moisture was nonlimiting, which is not typical of the sites where *P. ponderosa* is grown.

In this paper, we investigate the potential impact of changes in ambient O$_3$ in combination with changes in air temperature and atmospheric CO$_2$ concentrations on plant growth through a series of simulations using TREGRO, a process-based whole-tree growth model (Weinstein and Yanai 1994) parameterized for *P. ponderosa*, in which trees experienced a seasonal drought. We selected *P. ponderosa* var. *ponderosa* because it is: (1) widely distributed in the western U.S. (Fig. 1), (2) an economically important species, and (3) particularly sensitive to O$_3$. Specially we tested the hypotheses (1) that elevated CO$_2$ and temperature would alter the response of *P. ponderosa* to O$_3$ and (2) that seasonal drought would also reduce the effects of CO$_2$, temperature, and O$_3$.

METHODS AND MATERIALS

Study sites.—To represent a range of O$_3$ exposures, climate, and soil conditions, a latitudinal gradient within the *Pinus ponderosa* var. *ponderosa* zone (Oliver and Ryker 1990) in California, Oregon, and Washington was established (Fig. 1). The specific sites were selected because hourly O$_3$ data were available for all or most of a year and climate data were monitored at

TABLE 1. The current climate and soil characteristics for the sites used in the TREGRO tree $\times$ growth simulations.

Parameters	Crestline, CA	Sequoia, CA	Yosemite, CA	Lassen, CA	Jackson Co., OR	Crook Co., OR	Spokane Co., WA
Water year†	1990	1990	1990	1990	1990	1990	1990
Elevation (m)	1384	2054	1280	1788	503	1372	785
Latitude (° N)	34.24	36.60	37.54	40.54	42.16	44.13	47.49
Longitude (° W)	117.28	118.73	119.66	121.57	122.48	119.42	117.16
Mean air temperature (°C)	10.3	9.3	12.0	6.5	5.2	6.0	9.3
Mean soil temperature (°C)‡	12.8	7.6	13.8	8.5	7.0	7.7	10.8
Mean relative humidity (%)	49	63	39	62	65	63	72.6
Annual precipitation (mm)	1060	826	997	1108	1112	726	502
General soil texture	fine loam	coarse loam	sandy loam	loam	loam	loam	sility loam
Soil depth (A+B horizons) (cm)	81	104	61	84	64	152	43
Depth A horizon (cm)	18	30	28	48	30	84	20
Saturated hydraulic conductivity (cm/h)	1.6	2.0	6.0	3.4	1.0	3.3	1.1
Water content at field capacity (percentage dry mass)	27	25	22	23	34	37	41
Soil surface area (m²)§	75	50	50	75	75	75	75

Note: See Fig. 1 for state abbreviations.
† Water year is for the period 1 October through 30 September.
‡ The soil temperature is for the 5–50 cm layer
§ Soil surface area was adjusted to obtain a reasonable depletion of soil moisture and a late summer/fall drought stress.

either the site or nearby. Site locations and general climate and soil characteristics are listed in Table 1. Over the latitudinal gradient mean air temperature varied between 5.2° and 12.0°C and annual precipitation varied between 502 and 1108 mm.

Simulation model.—TREGRO, a process-based whole-tree growth model, was developed to examine the interactions between tree physiology, climatic and edaphic factors, and tropospheric O_3 (Weinstein and Beloin 1990, Weinstein et al. 1991). The model has been used to study the impact of O_3 on *Picea rubens* Sarg. and *Acer saccharum* growth (Laurence et al. 1993, Retzlaff et al. 1997), to test the O_3 sensitivity of different varieties of *P. ponderosa* (Constable and Taylor 1997), to study the relationships between O_3 exposure and plant phenology (Constable and Retzlaff 1997) and between O_3 exposure and drought (Retzlaff et al. 2000), and for assessing the effects of multiple stresses on plants (Weinstein and Yanai 1994). In all of these simulation studies, however, soil moisture was maintained at nonlimiting conditions.

In the model, growth is controlled by the availability of resources, particularly carbohydrates from the leaves and nutrients and water from the roots. While maximum daily growth rates are input parameters, growth may be less than these rates depending on the availability of resources and driving variables. Timing of growth in each compartment is controlled primarily through accumulation of degree-days, which permits trees from the various sites to have different growing season lengths and links their physiology to the local climate and soil conditions. In the present study, the simulations were run for a 3-yr period using the same weather and O_3 parameter files. To provide an estimate of the annual biomass (all plant components) increment, the total simulated biomass increase over the 3 yr was divided by three.

The model is initialized from parameter records that contain user-supplied biomass information, metabolic rates, maximum growth rates, and soil data. Biomass of the various compartments (leaves, branches, stem, coarse roots, and fine roots) is divided into total nonstructural carbohydrates (TNC), living tissue (structure), and wood as appropriate. Growth is based on the amount of structure present. The model uses several types of parameters to control the simulated response: maximum growth rates for each compartment, phenological response, maintenance and growth respiration rates, photosynthetic response, water movement, and nutrient uptake. In addition, there are parameters that describe the soil properties, including volume, nutrient levels, and water availability. The driving variables are air temperature, relative humidity, irradiance, precipitation, and O_3, and they are included in a file that has values for each 1-h interval of the simulation. The CO_2 concentration can be set to the desired concentration, but the concentration remains constant for any given simulation. The soil nutrient levels were the

same among sites and simulation runs, as site-specific soil nutrient concentrations were difficult to find and to facilitate the analysis of the temperature, CO_2, and O_3 effects, which was the objective of the simulations. As a consequence of interactions between precipitation, evapotranspiration, and soil physical properties, the onset and magnitude of the seasonal drought is unique for each site.

The model was parameterized using data from several sources. The biomass data were estimated from allometric equations for southern Oregon, USA (Hann and Scrivani 1987, Walters and Hann 1985, Hann and Larsen 1987, 1991) for a 30 cm DBH, 12 m tall tree. Leaf area was estimated from sapwood area using the method of Waring et al. (1982). The allometric equations were used to estimate the biomass of the various components in yearly time steps and growth rates were calculated from those estimates. This information was used both to set the initial biomass and growth rates for the simulation and to compare with the model results.

Parameters controlling photosynthesis were set initially to those reported by Clark et al. (1995). The maximum rate of carboxylation, $V_{\max}$, was then adjusted until simulated rates of photosynthesis in the youngest needle age class matched field observations made by N. E. Grulke (*personal communication*) on similarly sized trees. Photosynthesis in older needles was reduced to match observed values. Base respiration of growing tissues was set to 20% of the total daily carbon available for growth. Nonleaf maintenance respiration was set at 0.025% of the mass of structure per day. Actual rates were the result of a Q function with a doubling temperature of 10°C and a base of 20°C. Degree-day accumulations related to phenological events were based on observations of trees made at our location in Corvallis, Oregon.

The criteria used to evaluate the base parameterization were: (1) simulated maximum net daily photosynthetic rates within 10% of those measured in healthy trees by N. E. Grulke (*personal communication*) during the period without drought stress, (2) production of biomass ≤10% of that estimated from the allometric equations; (3) <10% year-to-year variation in the ratio of fine roots to needles and of root to shoot, (4) <10% year-to-year variation in TNC at the end of each year, and (5) development of a drought stress toward the end of each growing season and a drop in the soil water potential. TREGRO simulates water movement in the soil but only within the user-defined soil volume. Consequently it was necessary to adjust the soil volume to provide sufficient water throughout the season, while at the same time producing a late summer/fall drought stress. Once the model produced an appropriate simulation for the Jackson County, Oregon, site, the parameter set was adjusted for the other sites by changing the soil physical properties to reflect site specific conditions (Table 1) and the soil surface area was varied

to obtain a reasonable depletion of soil moisture (criterion 5) and a late summer/fall drought stress as indicated by a pattern of soil water content matching those modeled with the MAPPS model. Parameters directly controlling tree growth and metabolism were not changed among sites. Because measured seasonal soil moisture data were not available for the sites, simulated soil water potential values from the MAPPS model (Neilson 1995, Neilson and Marks 1994) were used to insure that the soils did not dry too rapidly; the soil rooting volume was adjusted to yield seasonal soil water potential patterns similar to those estimated from the MAPPS model. In most of the model runs, the module that allows soil moisture to affect photosynthesis and growth was used; however, in some instances this module was set to provide constant, nonlimiting, water. These latter runs were used to assess the importance of the yearly water stress on the final response.

While we recognize that there are ecotypic differences in pines from such diverse areas, we made the simplifying assumption that the parameter set developed for southern Oregon would adequately reflect *P. ponderosa* var. *ponderosa* response at all sites along the latitudinal gradient. This assumption allowed us to concentrate on the site-to-site variability in edaphic and climatic conditions and the various scenarios used in this study.

Soil characteristics.—As the necessary soils data were not available for the sites, they were obtained from the state soil geographic data base (STATSGO) dated October 1994 (Soil Conservation Service 1993). The soil chosen for each site was the most extensive soil component within the map unit that also had an entry in the STATSGO forest interpretations data table. General soil characteristics are listed in Table 1. Particle densities were inferred using the assumption that typical soil particle density is 2.6 g/cm^3 while volcanic soils are slightly less dense, 2.3 g/cm^3 (Brady 1974). The soil matric potential at air entry and the saturated hydraulic conductivity were calculated from particle size distribution data (Saxton et al. 1986). Approximate water content at field capacity (-33 kPa) was derived from particle size distribution and organic matter content (Rawls et al. 1982). Water holding capacity was estimated from the difference in water content at -33 kPa and -1500 kPa (Rawls et al. 1982). The soil water parameter B was calculated as the slope of the line relating the natural logarithm of the water potential and the natural logarithm of the water content between -4 kPa and -1500 kPa, calculated from particle size distribution and organic matter data (Rawls et al. 1982).

Soil temperatures (Table 1) were estimated from air temperature, solar radiation, and precipitation for a surface litter layer (0–5 cm), a surface soil layer (5–50 cm), a lower soil layer (50–150 cm), and a deep thermal damping layer (below 150 cm), based on the soil hydraulic and textual properties using a simplified one-dimensional heat transfer model (Philip and de Vries 1957).

Current climate scenario.—Co-monitored climate and O$_3$ data were available from the U.S. National Park Service for Sequoia and Lassen National Parks and for Crestline from the South Coast Air Management District in California. For the other sites where climate was not co-monitored, climate data were estimated using methods developed by Marks et al. (1993). Daily maximum and minimum air temperatures and precipitation were obtained from National Weather Service and Natural Resource Conservation Service SNOTEL sites (National Climate Data Center 1990, USDA Soil Conservation Service 1988, EarthInfo 1990*a, b*). Water year 1990 data were used for five sites, while only 1992 and 1989 data were available for Yosemite and Sequoia sites, respectively. After correction for elevation effects, hourly temperatures were estimated by fitting a sine function to the daily maximum and minimum temperatures, assuming a 4 AM minimum and a 4 PM maximum.

Because humidity tends to be more stable than temperature in mountainous regions of the western U.S. (Marks and Dozier 1979), relative humidity was estimated by assuming that the daily minimum temperature was approximately equal to the dew point temperature (Hungerford et al. 1989). This method works well during cooler seasons, and at higher elevations, but may fail during the warmest times of summer. Though only a few measurements of relative humidity were available, they were used to check, and if necessary, correct the relative humidity estimates.

Hourly clear-sky solar irradiance was simulated over a digital elevation model (DEM) (Marks et al. 1991) and corrected for both terrain structure and horizon effects. The model is based on work of Dozier (1980), and improvements by Dubayah et al. (1990), and Dubayah and Van Katwijk (1992). While this method accounts for solar geometry, atmospheric aerosol, and terrain effects on incident solar radiation over a region, it does not adjust for cloud effects. Hourly irradiance values were integrated to derive cumulative daily clear-sky solar radiation estimates, and the modeled daily radiation values were adjusted for each DEM grid point using maximum and minimum daily temperature surfaces to account for cloud cover (Bristow and Campbell 1984, Hungerford et al. 1989).

An orographic, moving-window linear regression model (Daly et al. 1994), used in conjunction with a DEM (NOAA 1989) and daily point measurements of precipitation, was used to estimate the precipitation over the western U.S. Daily estimates of site precipitation were derived from these elevation-corrected precipitation estimates. All precipitation was treated as "liquid"; daily precipitation was subdivided into equal hourly increments over a 6-h interval.

Current O$_3$ scenario.—Seven O$_3$ monitoring sites within the *P. ponderosa* growing region (Fig. 1) were

TABLE 2. The measured ambient O_3 exposures and the predicted O_3 concentrations for the various scenarios used in the TREGRO simulations for each site.

O_3 exposure parameters	Crestline, CA	Sequoia, CA	Yosemite, CA	Lassen, CA	Jackson Co., OR	Crook Co., OR	Spokane Co., WA
AIRS site ID	060710005	061070006	060430004	060893003	410290010	410130111	530630046
Year	1990	1990	1990	1990	1990	1983	1990
$0.8 \times$ Ambient [μmol/mol]h	200	67	41	12	7	3	2
$1.0 \times$ Ambient [μmol/mol]h	225	114	68	23	14	9	5
$1.1 \times$ Ambient [μmol/mol]h	237	138	82	31	19	14	7
$1.3 \times$ Ambient [μmol/mol]h	262	184	110	49	29	30	14

Notes: O_3 exposure is expressed as the W126 (sigmoid weighted exposure) index (Lefohn et al. 1988) summed for 8 mo (March through October) to provide a biologically relevant exposure value. The $1 \times$ ambient (i.e., measured O_3 exposure) data are from EPA's Aerometric Information Retrieval Service (AIRS) database. The number preceding ''ambient'' is the multiplier that was used to modify each hourly concentration according to Eq. 1. See Fig. 1 for state abbreviations.

identified to provide the O_3 exposures for the model simulations. Based on the O_3 monitoring data used in the simulations, only the Crestline site exceeded the U.S. National Ambient Air Quality Standard for O_3. TREGRO uses hourly O_3 concentrations in calculations of uptake and effects on photosynthesis; however, to summarize the season-long exposure, and to add biological relevance, we characterized the exposures (Table 2) using the W126 index (Lefohn et al. 1988). Ozone data were obtained from EPAs Aerometric Information Retrieval System data base. Missing hourly O_3 concentrations were imputed using two different approaches. (1) When ≥20 hourly concentrations were missing they were replaced with values from a randomly selected day with complete data from within that month. Because meteorological variables were unavailable for matching incomplete days and complete days, random pairing was used to impute the O_3 concentrations for incomplete days. (2) When there were <20 hourly concentrations missing, missing values were categorized by the run length number of missing 1-h periods. When ≤4 1-h periods were missing, values were replaced by the hourly concentrations immediately before and after the first and last 1-h period in the sequence. A sequence of missing values of ≥5 h was replaced by the previous or following day's hourly concentrations for those 1-h segments. We assumed that the diurnal patterns were similar from day to day within a month.

Future climate scenarios.—The Intergovernmental Panel for Climate Change (IPCC) (Houghton et al. 1992) suggests that temperatures will increase 0.2–0.5°C/decade with the best estimate being 0.3°C/decade. However, these projected temperature increases do not include the cooling effects of anthropogenic aerosols. An analysis of the instrumental record (using microwave sounding units, radiosonde data, and surface stations) suggests a temperature increase of 0.06–0.18°C/decade (Houghton et al. 1992). A warming of 1.3°C was selected, based on the IPCC scenario IS92a, and it is within the range recently suggested for the Pacific Northwest (JISAO/SMA Climate Impacts Group 1999). As the air temperature increases, the at-

mosphere's water holding capacity increases producing an increase in the moisture content of the atmospheric boundary layer (Houghton et al. 1992). As a first approximation of the increased atmospheric water content, the relative humidity (RH) was maintained constant between current and future climate scenarios (Houghton et al. 1992). Solar radiation and precipitation were unchanged between the climate scenarios. The soil temperature inputs for the model were based on air temperature scenarios and were simulated for each site.

In 1990 the global CO_2 concentration averaged 353 μmol/mol, and it is increasing at 1.8 μmol·mol^{-1}·yr^{-1} or 0.5%/yr (Houghton et al. 1992). At these rates, the atmospheric CO_2 is projected to increase to 443–453 μmol/mol in 2040. Based on the IPCC scenario IS92a, a CO_2 concentration of ~510 μmol/mol is expected by 2040 (Houghton et al. 1992). Given the range of possible outcomes we selected 500 μmol/mol as the future CO_2 scenario.

Future O_3 scenarios.—Over the last few decades, O_3 concentrations have increased 1–2%/yr (Fishman 1991, National Research Council 1991) and concentrations are expected to continue to increase. Based on patterns of expected emissions, Hough and Derwent (1990) suggested that O_3 concentrations would increase 20–50% (between 1990 and 2020) in lower latitudes (36–42° N) while at high latitudes (48–56° N) concentrations would increase 10–28%. However, various control strategies may decrease future concentrations; between 1988 and 1997 U.S. EPA (1998) reported a 19% decrease in O_3 concentrations. Consequently, we assumed that future concentrations could increase by 10–30% or decrease by 20% over current hourly concentrations.

To create the various O_3 exposure scenarios, the following procedure was used for adjusting the measured hourly ozone concentrations:

$$Oz' = Oz \times [1 - (1 - f)Oz/(max\ Oz)] \qquad (1)$$

where Oz' = the adjusted hourly O_3 concentration, Oz = the measured hourly O_3 concentration, max Oz = highest hourly O_3 concentration, and f is the scale adjustment of the max Oz. For example, a 20% reduction

of the maximum concentration corresponds to $f = 0.8$ and a 10% increase of the maximum concentration corresponds to $f = 1.1$. This procedure uses a quadratic weighting in C_{oz} to adjust the difference between the concentration and the requested scaling of the hourly concentrations.

RESULTS

TREGRO sensitivity

Prior to studying the impacts of O$_3$ on *Pinus ponderosa* growth under current and future climate scenarios, we evaluated the sensitivity of the TREGRO model to changes in soil moisture, air temperature, and CO$_2$.

Soil moisture.—Over its geographic range, there are large seasonal changes in precipitation, and *P. ponderosa* growth is frequently limited by low soil moisture during late summer (Oliver and Ryker 1990). A series of simulations compared the annual growth of *P. ponderosa* when water was nonlimiting and when the trees experienced a seasonal drought. At 350 μmol/mol CO$_2$, seasonal drought reduced annual biomass increment, across the latitudinal gradient, by 30–60% (*data not shown*). Increasing the CO$_2$ concentration to 500 μmol/mol reduced the effects of the seasonal drought on the annual biomass increase by ~5%, i.e., the growth reductions ranged from 25 to 55% across the seven sites. The annual transpiration averaged 5% greater at 350 μmol/mol CO$_2$ than at 500 μmol/mol CO$_2$. The simulations established that the seasonal drought scenario was sufficient to limit growth at all sites, as is typical for *P. ponderosa* areas. Consequently, all subsequent TREGRO simulations were conducted using a seasonal drought.

Air temperature.—To estimate the optimum growth temperature at 350 or 500 μmol/mol CO$_2$, a series of simulations were run at air temperatures (0°, 1.3°, 2°, and 4°C) above and below the current annual air temperature, and the estimated annual biomass increase was fit with a quadratic polynomial equation for each site. There were no discontinuities in the data, and a quadratic model fit the data well. Typical measures of fit and precision and statistical inferences to test for site differences were not performed because the TREGRO model operates without stochastic error. At 350 μmol/mol, the optimum growth temperature was 1.1–3.2°C higher than the current annual air temperature at all sites, except Crestline where the current annual air temperature was the optimum growth temperature (Table 3). Increasing the CO$_2$ concentration to 500 μmol/mol increased the maximum growth temperature at four sites (Yosemite, Lassen, Jackson Co., and Crook Co.) by 0.2–0.7°C, while the other three sites showed no change or a slight decrease (0.2–0.3°C) in the optimum temperature (Table 3).

Carbon dioxide.—At all sites, the annual biomass increment increased linearly with increasing CO$_2$ con-

TABLE 3. The effects of two CO$_2$ levels on the temperature optimum for ponderosa pine growth at seven sites across the range of ponderosa pine.

		Optimum growth temperature (°C)	
Site	Annual air temperature (°C)	CO$_2$ 350 μmol/mol	CO$_2$ 500 μmol/mol
Crestline, CA	10.3	10.3	10.3
Sequoia, CA	9.3	12.5	12.3
Yosemite, CA	12.0	13.1	13.5
Lassen, CA	6.5	9.3	9.5
Jackson Co., OR	5.2	7.9	8.3
Crook Co., OR	6.0	8.2	8.9
Spokane Co., WA	9.3	10.8	10.5

Notes: A quadratic polynomial was fit to the a range of annual air temperatures above and below the current annual air temperature to estimate the maximum growth temperature. See Fig. 1 for state abbreviations.

centration, at either the current air temperature or the current air temperature + 1.3°C (Table 4). Plant response to increasing CO$_2$, as measured by the slope of the regression line of annual biomass increment and CO$_2$ concentration, differed among sites (Table 4). Simulated tree growth at Crestline showed the greatest response to increasing CO$_2$, at either temperature, while Sequoia showed the least response to increasing CO$_2$. To determine if the CO$_2$ response was different between temperature scenarios, we calculated the ratio of the slopes of the CO$_2$ response lines at elevated/ambient temperature (Table 4). This ratio tended to be larger at the sites with lower annual temperatures and to decrease as the annual temperatures increased. This pattern suggests an interaction between temperature and CO$_2$ that varies among sites.

Effect of elevated CO$_2$ and temperature on P. *ponderosa growth.*—Based on the simulations, annual *P. ponderosa* growth at Crestline was the largest (~35%

TABLE 4. The slopes of the linear regression equations relating annual total biomass to atmospheric CO$_2$ concentrations.

	Regression slope†		Ratio of the response to CO$_2$ at elevated vs. ambient temperature
Site	Ambient temperature	Ambient temperature + 1.3°C	
Crestline, CA	128.1	129.6	1.01
Sequoia, CA	58.1	62.1	1.07
Yosemite, CA	82.1	82.8	1.01
Lassen, CA	94.9	99.3	1.05
Jackson Co., OR	67.2	71.9	1.07
Crook Co., OR	72.9	77.4	1.06
Spokane Co., WA	81.4	81.0	0.99

Notes: The TREGRO model was used to simulate plant response to a range of atmospheric CO$_2$ (350–750 μmol/mol) at ambient air temperature for each site and for the ambient temperature increased by 1.3°C. See Fig. 1 for state abbreviations.

† The slope of the regression line has the units of annual biomass increase/CO$_2$ concentration.
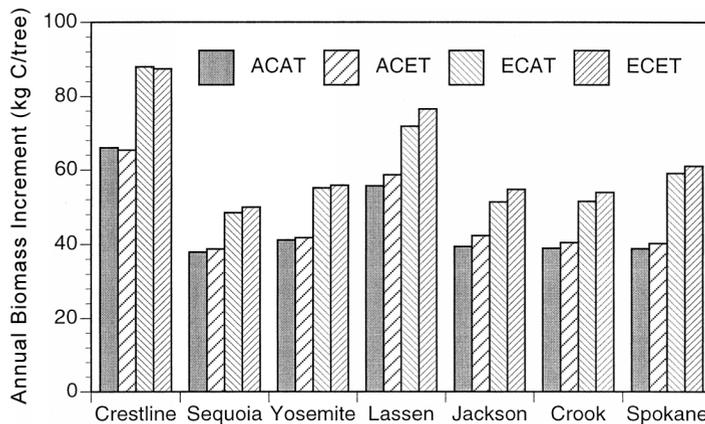
Fig. 2. Effects of elevated CO_2 and temperature on the annual biomass growth of *Pinus ponderosa* at selected sites across its range. The treatment abbreviations are: ACAT = ambient CO_2, ambient temperature; ACET = ambient CO_2, elevated (+1.3°C) temperature; ECAT = elevated (500 μmol/mol) CO_2, ambient temperature; ECET = elevated (500 μmol/mol) CO_2, elevated (+1.3°C) temperature.

larger than the mean of the remaining sites), and Sequoia had the smallest annual biomass increase (Fig. 2). The annual biomass increases at the Crook, Jackson, and Spokane sites were similar to each other. Increasing air temperature by 1.3°C reduced the annual biomass increase at Crestline (Fig. 2); this reduction is consistent with the previous simulation result (Table 3) that the current air temperature at Crestline is the optimum growth temperature. At the other six sites, increasing air temperature by 1.3°C increased the annual growth. Yosemite showed the smallest increase (~1.5%) to increasing temperature while Lassen and Jackson showed the largest increases (6–7%). As anticipated from the initial sensitivity simulations, increasing the ambient CO_2 concentrations from 350 to 500 μmol/mol increased annual growth at all sites (Fig. 2). Annual growth at Spokane displayed the largest increase (~50%) in response to increased CO_2, while Sequoia

had the smallest increase (~28%). The annual total-biomass increase at the rest of the sites ranged 30–34%.

Impact of elevated O_3 on annual growth

Ozone sensitivity.—To insure that TREGRO was sensitive to a range of O_3 exposures, simulations were performed at zero and ambient O_3 for each of the sites (Table 5). To estimate the O_3 effect, growth at the ambient O_3 was compared to growth in the absence of O_3 for each of the sites. Ozone exposures ranged between 5 and 225 (μmol/mol)h, and the percentage reduction in annual biomass increment ranged from 0.1 to 47%, with the percentage reduction increasing with O_3 exposure. Crestline displayed the largest percentage reduction (47%) in annual biomass growth, ~5× larger than Sequoia, the next largest site. Excluding Crestline, the percentage reduction in annual biomass increased linearly with increasing O_3 exposure.

Ozone impact.—Simulations were performed at each site to determine the effect of various O_3 exposures and CO_2 and temperature scenarios on annual biomass increments. For each combination of CO_2 and temperature, a linear regression model was used to relate the percentage change in growth (relative to growth at ambient O_3 exposure) to the given O_3 exposure (Fig. 3A). The slope of the regression line shows the percentage change in O_3 response for a unit change in O_3 exposure. For example, the slope of the regression line for Lassen is steeper (−0.1516) than that for Sequoia (−0.0937) showing that a unit change in O_3 exposure has a greater impact on the annual growth increment at Lassen than at Sequoia (Fig. 3A). A unit (1 [μmol/mol] × h) increase in O_3 exposure at Lassen is predicted to reduce the annual biomass growth by ~0.15%/yr while a unit decrease in O_3 exposure would increase annual biomass growth by ~0.15%/yr.

The slope of the linear regression line, which related the percentage change in growth to the O_3 exposure (Fig. 3A) for each combination of CO_2 and temperature, was used to compare O_3 sensitivity among sites and

TABLE 5. The predicted reduction in the annual biomass increment, expressed as the percentage reduction in the annual biomass increment caused by exposure to ambient O_3 compared to the annual biomass increment in the absence of O_3.

Site	Ambient O_3 exposure ([μmol/mol] × h)†	O_3 effect (percentage reduction)‡
Crestline, CA	225	46.86
Sequoia, CA	114	8.93
Yosemite, CA	68	5.15
Lassen, CA	23	2.53
Jackson Co., OR	14	1.31
Crook Co., OR	9	0.06
Spokane Co., WA	5	0.16

Notes: The TREGRO model was used to simulate plant response to a O_3 at ambient CO_2 and ambient air temperature for each site. See Fig. 1 for state abbreviations.

† O_3 exposure is expressed as the W126 (sigmoid weighted exposure) index (Lefohn et al. 1988) summed for 8 mo.

‡ The O_3 effect is expressed as the percentage reduction in the annual biomass increment caused by exposure to ambient O_3 compared to the annual biomass increment in the absence of O_3.
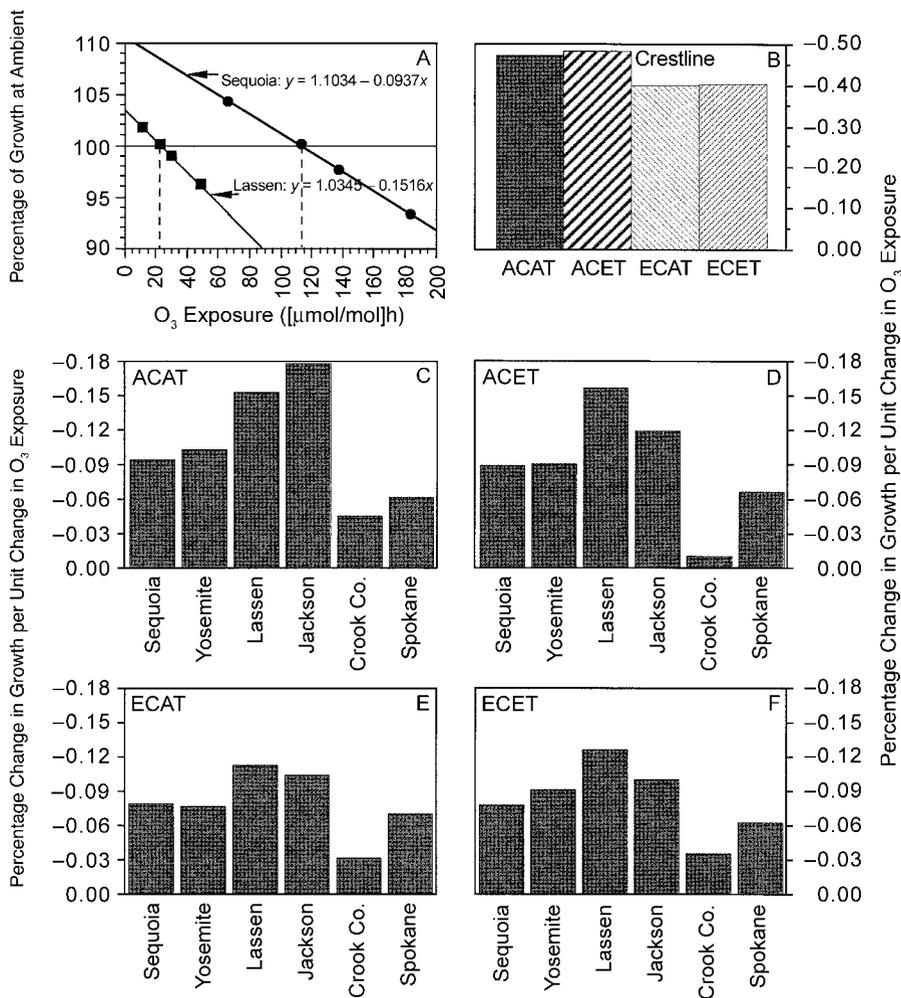
Fig. 3. Effects of elevated CO$_2$ and temperature on the response of *Pinus ponderosa* to a range of O$_3$ exposures. (A) The percentage difference in growth at a given O$_3$ exposure compared to growth at the ambient O$_3$ exposure for two sites. The light solid line shows the 100% growth response, and the dashed lines from the 100% line show the ambient O$_3$ exposure at each of the two sites. The slopes of the lines show the percentage change in O$_3$ response for a unit change in O$_3$ exposure. The slope values for the various sites and treatment conditions are shown in panels (B)–(F). The treatment abbreviations are as in Fig. 2.

CO$_2$ and temperature scenarios (Fig. 3B–F). The simulations established that the trees at Crestline displayed a greater change in response to a unit change in O$_3$ exposure than did the trees at the other sites; consequently, the data for Crestline were displayed in a separate figure (Fig. 3B). At Crestline a unit change in O$_3$ exposure changed annual biomass increment 0.4–0.5%, while at the other sites the changes in annual biomass increment ranged from 0.02 to 0.18% for a unit change in O$_3$ exposure. Under current climate conditions, the other six sites tended to group into pairs (Fig. 3C). The trees at Lassen and Jackson were the most sensitive to changes in O$_3$ exposure while the ones at Crook Co. and Spokane were the least sensitive. Among the sites, O$_3$ sensitivity increased with increasing precipitation and tended to decrease with increasing temperature.

At ambient temperature, increasing the CO$_2$ concen-

tration reduced the O$_3$ impact at all the sites except Spokane, where it was essentially unchanged (Fig. 3B, C, and E). At ambient CO$_2$, increasing the temperature decreased the O$_3$ impact at four of the sites, and the sensitivity remained unchanged at Crestline, Lassen, and Spokane (Fig. 3B–D). Increasing both CO$_2$ and temperature decreased (compared to the current temperature and CO$_2$ scenario) the O$_3$ impact at all sites except Lassen and Spokane, where it was unchanged (Fig. 3B, C, and F). In these altered temperature and CO$_2$ scenarios, precipitation remains the principal factor controlling O$_3$ impacts among sites with air temperature having a lesser influence.

DISCUSSION

Models provide a conceptual basis for: (1) integrating diverse measures into a selfconsistent framework,

(2) relating stressors to probable effects, and (3) making meaningful extrapolations across scales of time, space, and biological organization (Suter 1993, Rapport 1992, Rastetter 1996). In nature, synergistic interactions among various environmental factors, such as temperature, precipitation, nutrient levels, topography, and soil moisture, make it impossible to predict or assess future responses of plants to stressors, such as tropospheric O_3, elevated CO_2, or temperature, based on single-factor experiments alone (Rastetter et al. 1991). Process-based models can improve such assessments by providing a self-consistent synthesis of the results of many experiments. The synthesis provided by these models includes the interactions among processes that give rise to the synergistic responses to multiple factors.

Model sensitivity.—Experimental studies have shown that elevated CO_2 increased plant height, stem diameter, leaf area index, and fine root biomass of *Pinus ponderosa* (Johnson et al. 1998, Tingey et al. 1996; T. Ball, *personal communication*) and increased *P. ponderosa* growth (Pushnik et al. 1995, Surano et al. 1986). Based on a number of studies, Morison and Lawlor (1999) and Norby et al. (1999) concluded that although elevated CO_2 increases the carbon assimilation rate, it does not mean that growth will be increased because of possible limiting factors in natural ecosystems. In the simulations, plant growth increased proportional to the CO_2 concentration; however, the magnitude of the growth increase varied among sites as a function of changes in precipitation, air temperature, and growing-season length.

Both modeling and experimental studies have shown that elevated CO_2 increases the temperature optimum for photosynthesis (Long 1991, Sage et al. 1995, Morison and Lawlor 1999). These results led to the suggestion that elevated CO_2 could alleviate high temperature stress via increased assimilation (Morison and Lawlor 1999). In our simulations, elevated CO_2 increased the temperature optimum for growth at four sites and decreased it at two sites. The variable effect of increasing CO_2 on the growth-temperature optimum are the result of the interactions of temperature (air and soil), soil moisture, and growing-season length within the TREGRO modeling framework.

P. ponderosa is widely distributed across the western United States, and western (var. *ponderosa*) and eastern (var. *scopulorum*) varieties are recognized (Oliver and Ryker 1990). The varieties differ in physiology, morphology, and growth and a study using TREGRO suggested that the western variety found in California, Oregon, and Washington is more sensitive to O_3 than the eastern variety (Constable and Taylor 1997). The western variety grows where there are large seasonal changes in precipitation, and plant growth is frequently limited by low soil moisture during late summer. This is an important feature to capture in simulations of changes in O_3 response with changes in temperature

and elevated CO_2. Constable et al. (1996) used TREGRO, without seasonal drought, to study the effects of elevated CO_2 and temperature on the response of *P. ponderosa* to O_3. They reported that O_3 (W126 O_3 exposure index = 62 [μmol/mol] × h) reduced annual biomass increment 19%, while in our simulations, with a water limitation, O_3 reduced the annual biomass increment ~9% at a W126 O_3 exposure index of 114 (μmol/mol)h and ~5% at W126 O_3 exposure index of 68 (μmol/mol)h. The inclusion of a seasonal drought in the simulations significantly reduced the effect of O_3. Our simulations are consistent with empirical studies in which drought reduces O_3 uptake and decreases O_3 effects on plants. For example, reduced water availability decreased O_3 injury in both seedling and mature *P. ponderosa* (Temple et al. 1992, Temple and Miller 1996). Using a different simulation model Chen et al. (1994) also reported that drought reduced the impact of O_3 on the growth of *P. ponderosa*. A TREGRO study of the effect of drought and O_3 on the growth of *Abies concolor* (Gord. & Glend.) Lindl. Ex Hildebr. growing in the Sierra Nevada of California (Retzlaff et al. 2000) found that high levels of drought reduced the impact of O_3 but that moderate amounts of O_3 and drought reduced growth more than either stress singly.

Ozone response.—Although a model simulation cannot establish that growth was actually reduced by O_3 exposure, it can provide suggestive evidence that O_3 is a factor reducing growth in an area. Using tree cores collected from sites along a north–south gradient in the Sierra Nevada of California, Peterson et al. (1991) assessed the impact of regional O_3 exposure on *P. ponderosa*. They reported that O_3 symptoms decreased from south to north, following the O_3 exposure gradient (e.g., Table 2, Peterson et al. 1991). Using a large range of sites throughout the Sierra Nevada and the San Bernardino Mountains, Arbaugh et al. (1998) established that foliar injury on *P. ponderosa* and *P. jeffreyi* increased with increasing O_3 exposure. Although Peterson et al. (1991) detected no regional scale growth reductions attributable to O_3, they did find significant growth reductions in some *P. ponderosa* stands in the southern Sierras (e.g., Sequoia). The largest growth reductions occurred in areas with the highest O_3 exposure and the most O_3 symptoms on the needles. In the Sequoia and Kings Canyon National Parks, Peterson et al. (1987) reported that the annual radial growth of *P. jeffreyi* trees displaying foliar O_3 injury was 11% less than for asymptomatic trees. Over a similar range of sites, our simulations suggest that O_3 reduced the annual biomass increment 8.9–2.5% (south to north) and followed the same spatial pattern of foliar injury as that report by Peterson et al. (1991) and Arbaugh et al. (1998). Given the relatively small reductions in annual biomass along the Sierra gradient, it is not surprising that Peterson et al. (1991) had difficulty in detecting a consistent O_3 effect on growth against the

variation in growth introduced by other factors in the environment.

Ozone impact.—The trees at Crestline received the highest O$_3$ exposure, and the simulations indicates that these trees experience the largest O$_3$ impact. The area has experienced high O$_3$ exposures for several decades; tree decline and the loss of sensitive individuals has already occurred (Miller and McBride 1999). The Crestline site is near the southern limit for the western variety of *P. ponderosa* (Fig. 1). The simulations suggest that the temperature at Crestline is near the optimum (i.e., higher temperatures decreased growth) for *P. ponderosa*; the higher temperatures increased respiration, depleting carbohydrate reserves. Constable and Taylor (1997) reported that mature *P. ponderosa* growing in stressed sites (i.e., where their carbohydrate reserves were depleted) were particularly susceptible to O$_3$.

Among the other sites, Lassen and Jackson Co. displayed the highest O$_3$ sensitivity although their O$_3$ exposures were relatively low. The differences in sensitivity among sites are primarily controlled by differences in precipitation. There is a strong linear relation ($r = 0.87$) between percentage change in growth and annual precipitation, but only a weak relationship ($r = 0.36$) with annual mean air temperature. The Lassen and Jackson Co. sites are relatively mesic with high precipitation while the Crook Co. and Spokane Co. sites were the least sensitive and received the least precipitation.

A key question is, will changes in CO$_2$ and temperature alter O$_3$ impacts on *P. ponderosa*? In a simulation study using *P. ponderosa* and no water limitation, Constable et al. (1996) reported that elevated CO$_2$ and elevated temperature ($+4°C$), singly and in combination, increased plant growth. Individually, elevated CO$_2$ and elevated temperature reduced the impact of O$_3$ on growth and, the combined effects of CO$_2$ and temperature eliminated the O$_3$ impact. Their results are consistent with empirical studies in which elevated CO$_2$ reduces O$_3$ uptake and decreases O$_3$ effects on plants (U.S. EPA 1998). Similarly, in our simulations, with a water limitation, increasing CO$_2$ decreased O$_3$ sensitivity at all sites. Increasing CO$_2$ decreased transpiration 5% and was associated with a decrease in O$_3$ impact, suggesting that the stomatal conductance was decreased, limiting O$_3$ uptake. However, the effect of increasing temperature on O$_3$ sensitivity was less consistent in simulations with a seasonal drought than in simulations without one (Constable et al. 1996). Increasing temperature did not always reduce the O$_3$ impacts.

TREGRO simulates the response of a tree to ozone by decreasing mesophyll conductance according to a user-specified function. By adjusting the slope of the linear function, the user can adjust the effect until the modeled photosynthesis matches that hypothesized, or in our case, the observed rate of photosynthesis at a given ozone exposure. Needles accumulate an "ozone dose," a measure of total uptake, using the hourly ozone concentration and the stomatal conductance, which is calculated by reducing a maximum rate of conductance according to light, vapor pressure deficit, and soil moisture conditions. There is no mechanism for reducing stomatal conductance as a function of ozone exposure. Similarly, there is no feedback in photosynthesis to reduce stomatal conductance in the presence of excess CO$_2$ or due to large quantities of allocable carbon. To overcome this limitation, fixed carbon in excess of that needed for growth, for respiration, or to fill storage compartments, is made inaccessible to the tree for future use. Stomatal conductance is used in the calculation of daily transpiration, but is not available as an output in the model.

Implications for tree growth.—The interactions of tropospheric O$_3$, changing temperature, and rising atmospheric CO$_2$ can alter forest growth. Our simulations suggest that increasing CO$_2$ will increase tree growth, even if there is a seasonal drought. Also, current and increasing levels of tropospheric O$_3$ can decrease tree growth. However, rising atmospheric CO$_2$ concentrations can partially offset the current decreases in tree growth from O$_3$ exposure. Although increasing CO$_2$ reduces O$_3$ impact, elevated CO$_2$ would enhance plant growth more if O$_3$ exposures were reduced, especially in the more polluted sites. Although the greatest benefit to tree growth will come from reducing O$_3$ exposure in the most polluted sites, we must also consider those sites that have inherent high O$_3$ sensitivity because of their mesic conditions and limit the growth of O$_3$ exposures in those areas also. In contrast, tree growth in other areas would likely not be as impacted by increasing O$_3$ exposures because the plants are climatically less sensitive to O$_3$.

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