# Interactive Effects of $O_3$ and $CO_2$ on the Ponderosa Pine Plant/Litter/Soil System

### *Statement of the Problem*

Carbon dioxide is required by plants to grow and is a major greenhouse gas contributing to global climate change. Tropospheric ozone ($O_3$) is the major phytotoxic air pollutant in the U.S. which adversely impacts crops and forests. While much is known about the effects of $O_3$ or $CO_2$ alone, there has been little research on the potential interactive effects of these gases on terrestrial ecosystems, even though they co-occur. Most of the research has focused on the response of individual species rather than at the ecosystem level. There is a growing interest in $O_3$ x $CO_2$ combinations fueled by concerns regarding potential effects on vegetation from increases in regional $O_3$ levels. These increases occur concurrently with an increased global $CO_2$ concentration.

### Approach

Therefore, we carried out an in-depth study to address three general hypotheses regarding the effects of $O_3$ and $CO_2$ on C, N, and $H_2O$ cycling through ecosystems (Olszyk *et al.* 1997):

1) Elevated $O_3$ decreases C, N and $H_2O$ cycling rates.

2) Elevated $CO_2$ increases C, N, and decreases $H_2O$ cycling rates.

3) Elevated $CO_2$ eliminates negative effects of $O_3$ on C and N cycling rates and has an additive negative effect on $H_2O$ cycling rates.

Our hypotheses were tested using experimental data and simulation models to evaluate C, N, and $H_2O$ cycles (Olszyk *et al.* 2001). A reconstructed ponderosa pine soil/tree seedling ecosystem was used, as this is system widespread in the western U.S., and is known to be affected by both increasing $CO_2$ and $O_3$. The experiment was conducted in sunlit, controlled environment chamber facility (see sidebar in previous section) to examine above- and belowground responses. These chambers allowed for precise monitoring and control of climatic and edaphic—soil—conditions and for calculation of whole system $CO_2$ and $H_2O$ balances (Tingey *et al.* 1996, Olszyk and Tingey 1996). The experimental design was a 2 x 2 factorial with 2 levels of $CO_2$, 2 levels of $O_3$ and three replicate chambers per treatment. Carbon dioxide was an elevated level of +280 ppm above ambient reflecting an increase in greenhouse gases vs. the ambient concentration. Ozone was at a high level representative of regional oxidant pollution vs. a low level which is representative of a more pristine area. Research tasks measured: i) system $CO_2$, $O_3$ and $H_2O$ gas exchange; ii) plant phenology, allometry and carbon allocation; iii) litter and soil/rhizosphere microbiological community structure and function; iv) litter and soil chemical and physical properties; and v) system C, N and $H_2O$ budgets, pools and fluxes. The modeling research used the Marine Biological Laboratory's General Ecosystem Model (GEM) (Rastetter *et al.* 1991) to evaluate for system scale C and N cycling, and the process-based whole-tree growth model TREGRO (Tingey *et al.* 2001), to study the potential impact of increased $O_3$ and $CO_2$ on photosynthesis, respiration, carbon accumulation, and carbon allocation.

**Main Conclusions**

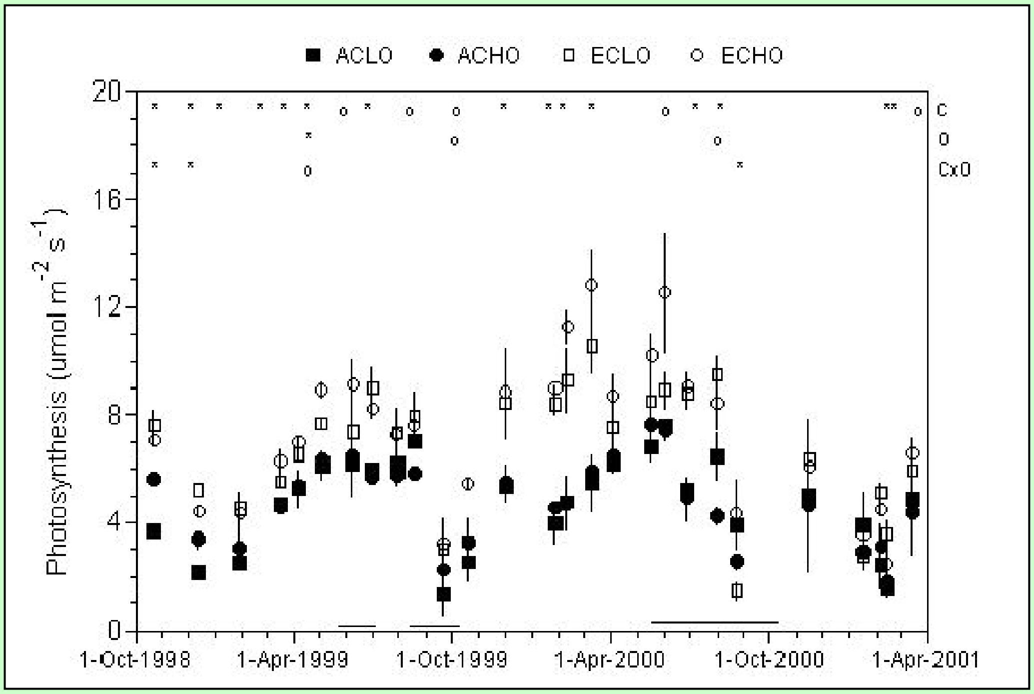
Elevated $CO_2$ increased the photosynthetic C uptake by the seedlings beginning early in the study (Olszyk *et al.* 2001) and persisting to the end (Olszyk *et al.* 2002) (sidebar). The increase in photosynthesis was associated with an increase in water use efficiency (the ratio of $CO_2$ taken up to $H_2O$ loss by transpiration). The increased C uptake appeared to stimulate plant growth as elevated $CO_2$ increased stem diameters (sidebar). This $CO_2$ induced-increase in stem diameter was especially noticeable early during the study. Over time, the stimulation in stem diameter leveled off, possibly due to growth-limiting factors such as a low soil-N fertility level. Elevated $CO_2$ also affected N cycling in the system as indicated by lower leaf N concentrations with elevated $CO_2$ (Olszyk *et al.* 2001).

In contrast to $CO_2$, $O_3$ alone had little effect on the plants, and those responses that did occur were affected by the variable $O_3$ concentrations among the three years. There were suggestions of significant $CO_2$ x $O_3$ interactions for some parameters where the response to the combined pollutants was different from that expected based on the responses to the individual pollutants. For example, in late August 2000 photosynthesis decreased with high $O_3$ for seedlings at ambient $CO_2$ but increased with high $O_3$ for seedlings at elevated $CO_2$. There also was a significant $CO_2$ x $O_3$ interaction on plant growth early in the study, as stem diameters were greater with elevated $CO_2$ and low $O_3$ compared with elevated $CO_2$ and high $O_3$ (Olszyk *et al.* 2001).

When the data have been completely evaluated from this study, the results will provide unique information on the responses of ecosystem functions due to the interactions of $CO_2$ and $O_3$, as well as responses to the individual gases.

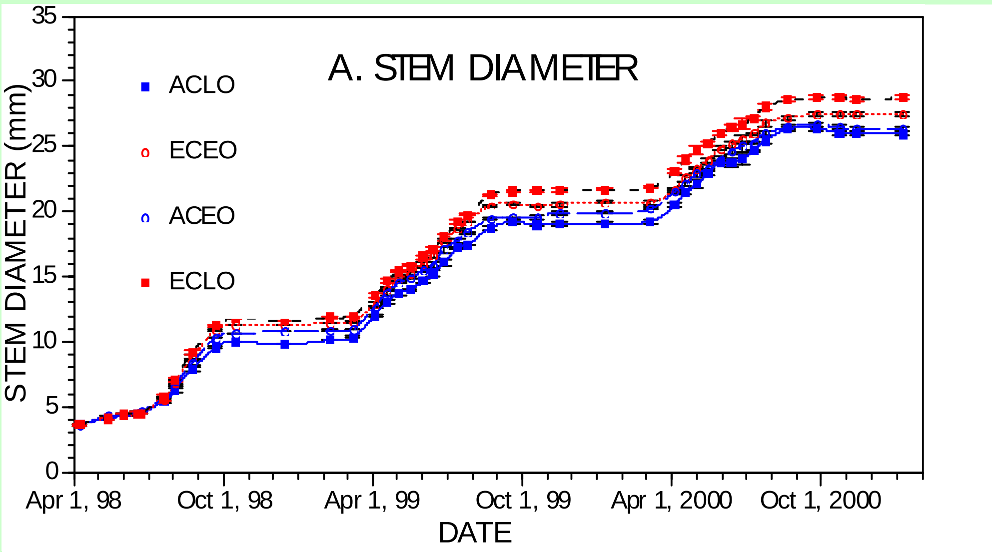
## Effects of Elevated $CO_2$ and $O_3$ on Net Photosynthesis in Ponderosa pine

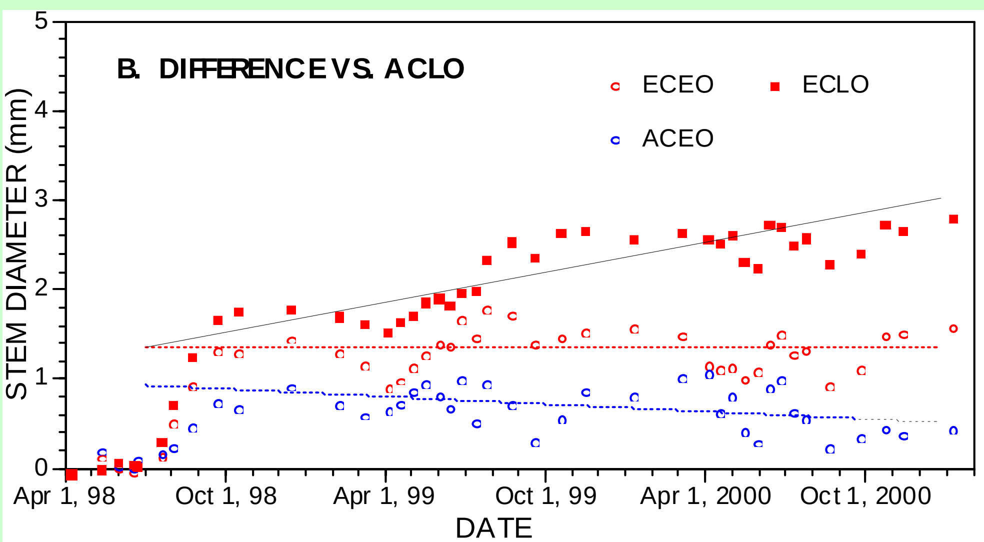
Elevated $CO_2$ increased photosynthetic rates over much of the experiment as shown by the higher values for seedlings grown under elevated $CO_2$ at either low $O_3$ (ECLO) or elevated $CO_2$ and high $O_3$ (ECHO) *vs.* seedlings grown under ambient $CO_2$ and either low $O_3$ (ACLO) or high $O_3$ (ACHO. The "*" and "o" symbols in the "C" row at the top of the figure indicate those periods during which there was a significant $CO_2$ effect on photosynthesis based on analysis of variance at the $p<0.05$ and $p<0.10$ levels, respectively. High $O_3$ had only a minor effect on photosynthesis, with significant $O_3$ alone effects for only three periods as shown by the symbols in the "O" row at the top, and significant $CO_2$ x $O_3$ interactions for only 4 periods in the "CxO" row at the top. The symbols are averages "SE (bars) for 3 replicate chambers except for 2 replicate chambers for the treatment. The dashed lines at base of figure are approximate dates of $O_3$ exposures. Source: Olszyk *et al.* 2002.



## Effects of CO2 & O3 on Ponderosa Pine Seedlings

Stem diameter was measured as a key indicator of the overall growth of Ponderosa pine seedlings. Rapid growth periods, as shown by an increase in stem diameter, occurred during spring and summer of 1998, 1999, and 2000. Over three years, seedlings growing with elevated $CO_2$ and either with low (ECLO) or high (ECHO) $O_3$, had larger stem diameters than seedlings grown under ambient $CO_2$ and low (ACLO) or high (ACHO) $O_3$ (top figure). Beginning early in the study, compared to plants growing under control conditions (ACLO), there was a greater increase in stem diameter for ECLO compared with ECHO seedlings, indicating that high $O_3$ inhibited some of the effect of elevated $CO_2$ (lower figure). Source, Olszyk *et al.* 2001and unpublished data.



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Olszyk, D.M., Tingey,D.T., Johnson , M. G.,, Seidler, R., Watrud, L., Weber, J., Phillips, D., & Andersen, C., Cairns, M., Hogsett, W., Brown, S.and McKane, R. 1997. Research Plan: Interactive Effects of $O_3$ and $CO_2$ on the Ponderosa Pine Plant/Litter/Soil System. US EPA, NHEERL-COR-876R.

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Rudorff, B.F.T., Mulchi, C.L. & Lee, E.H. 2000. Plant Responses to Elevated $CO_2$ and Interactions with $O_3$. In Trace Gas Emissions and Plants. (ed. S.N. Singh). pp. 155-179. Kluwer Academic Publishers, Dordrecht, Germany.

Tingey, D. T., J. A. Laurence, J. A. Weber, J. Greene, W. E. Hogsett, S. Brown, and E. H. Lee. 2001. Elevated $CO_2$ and temperature alter the response of *Pinus ponderosa* to ozone: a simulation analysis. *Ecological Applications* 11:1412-1424.

## *Annotated Bibliography of WED Research*

**Beedlow, Peter A, David T Tingey, Donald L Phillips, William E Hogsett, and David M Olszyk. 2004. Rising atmospheric $CO_2$ and carbon sequestration in forests. *Front Ecol Environ* 2(6): 315–322.**

Rising $CO_2$ concentrations in the atmosphere could alter Earth's climate system, but it is thought that higher concentrations may improve plant growth through a process known as the "fertilization effect". Forests are an important part of the planet's carbon cycle, and sequester a substantial amount of the $CO_2$ released into the atmosphere by human activities. Many people believe that the amount of carbon that forests sequester will increase as $CO_2$ concentrations rise. An increasing body of research suggests, however, that the fertilization effect is limited by nutrients and air pollution, in addition to the well documented limitations posed by temperature and precipitation. This review suggests that existing forests are not likely to increase sequestration as atmospheric $CO_2$ increases. Therefore, it is imperative that we manage forests to maximize carbon retention in above- and belowground biomass and conserve soil carbon.

**Laurence, J. A., W. A. Retzlaff, J. S. Kern, E. H. Lee, W. E. Hogsett, and D. A. Weinstein. 2001. Predicting the regional impact of ozone and precipitation on the growth of loblolly pine and yellow-poplar using linked TREGRO and ZELIG models. Forest Ecology & Management 146:247-263.**

To simulate the long-term effects of ozone on forests in the US, we linked TREGRO, a mechanistic model of an individual tree, to ZELIG, a forest stand model, to examine the response of forests to 5 ozone exposure regimes (0 to ~100 ppm h SUM06 per year) in 100 year simulations. TREGRO and ZELIG were parameterized using biological and meteorological data from three climate sites in the southeastern US. TREGRO was used to generate three-year exposure-response relationships between ozone and growth of loblolly pine *(Pinus tae*da L.) and yellow-poplar (*Liriodendron tulipifera* L.). Ratios (response at ozone exposure: response at base case) of total tree mass, leaf mass, and fine root/leaf mass were calculated and used to modify growth functions in ZELIG. At the end of the ZELIG simulation, the change in basal area of loblolly pine ranged from an increase of 44 percent to a decrease of 87 percent, depending on precipitation and ozone exposure. The basal area of yellow-poplar, simulated in competition with loblolly pine was not affected over most of its range. Over the range of the two species, the simulated changes in basal area due to ozone exposure were generally within ±10 percent of the base case. Competitive interactions between the species were not altered.

**Olszyk, D. M., D. T. Tingey, L. Watrud, R. Seidler, and C. Andersen. 2000. Interactive effects of $O_3$ and $CO_2$: implications for terrestrial ecosystems *in***

**Climate Change and Plants/Trace Gas Emissions and Plants. Singh et al., editors. Pp 97-136, Kluwer Academic Publishers, The Netherlands.**

Ozone and $CO_2$ can have interactive effects on vegetation, with implications for terrestrial ecosystems. However, the combined impacts of both gases on vegetation are uncertain despite their co-occurrence. Thus, the objectives of this review are: (1) to evaluate the literature concerning interactive effects of $O_3$ and $CO_2$ on vegetation; and, (2) carry out this evaluation in the context of terrestrial ecosystem processes, i.e., carbon and nitrogen cycling. The literature indicates that: 1) there is no consistent interaction between $O_3$ and $CO_2$ on stomata; but an additive effect of $O_3$ and $CO_2$ which likely reduces the flux of both gases into leaves below the levels with the individual gases; 2) an increase in photosynthesis with elevated $CO_2$ may be canceled by a decrease in photosynthesis with high $O_3$; 3) elevated $CO_2$ inhibits $O_3$ induced leaf injury ; and, 4) interactions between $O_3$ and $CO_2$ can interact to affect storage carbohydrates, leaf free radical metabolism, and allocation of C to shoots and roots. The nature of the interactions between $O_3$ and $CO_2$ vary with parameter, species and experiment. Furthermore, the mechanisms by which $O_3$ and $CO_2$ interact physiologically and metabolically are very uncertain. There is little information on effects of $O_3$ and $CO_2$ on other aspects of the belowground system such as root/rhizosphere processes, litter and soil microbes, and litter and soil physical and chemical properties. Intensive ecosystem-level studies are needed to determine the combined effects of $O_3$ and $CO_2$ on terrestrial vegetation, focusing of C and N cycling.

**TAUSZ, M., D.M. OLSZYK, S. MONSCHEIN, and D.T. TINGEY. 2004. Combined effects of CO2 and O3 on antioxidative and photoprotective defense systems in needles of ponderosa pine. BIOLOGIA PLANTARUM 48 (4): 543-548,**

Ponderosa pine (*Pinus ponderosa* Dougl. *ex* Laws.) seedlings were exposed to near ambient or elevated CO2 (average concentrations during the last growing season 446 *versus* 699 µmol mol-1), combined with low or elevated O3 for three seasons. Ozone exposure during the last growing season (accumulated dose above threshold 0.06 µmol mol-1) was 0.05 *versus* 26.13 µmol mol-1 h. Needles of the youngest age class were harvested after the dormancy period. Ozone exposure decreased needle contents of chlorophyll *a*, chlorophyll *b*, and ascorbate, and resulted in a more oxidized total ascorbate and a more de-epoxidized xanthophyll cycle pool irrespective of the CO2 level. Trees under elevated CO2 had a more oxidized glutathione pool and lower chlorophyll *a* content. Contents of glutathione, tocopherol, and carotenoids were not affected by the CO2 or O3 treatments. There were no interactive effects between elevated CO2 and elevated O3 on any of the parameters measured. The results suggest that elevated atmospheric CO2 concentration does not compensate for ozone stress by increasing antioxidative capacity in ponderosa pine.
*Additional key words*: air pollution, ascorbate, glutathione, oxidative stress, pigments, *Pinus ponderosa*, xanthophyll.

**Tingey, David T., John A. Laurence, James A. Weber, Joseph Greene, William E. Hogsett, Sandra Brown and E. Henry Lee. 2001. Elevated $CO_2$ and temperature alter the response of *Pinus ponderosa* to ozone: a simulation analysis. Ecological Applications 11:1412-1424.**

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.

**Yoshida, Lidia C., John A. Gamon and Christian P. Andersen. 2001. Differences in above- and below-ground responses to ozone between two populations of a perennial grass. Plant and Soil 233:203-211.**

Our study examined the influence of elevated ozone levels on the growth and mycorrhizal colonization of two populations of *Elymus glaucus* L. (blue wildrye). We hypothesized that ozone would reduce carbon availability to the plants, particularly below ground, and would affect mycorrhizal colonization. Because of the wide geographic range of *E. glaucus,* two populations of plants were selected from areas of contrasting ozone histories to examine intraspecies variation in response to ozone. Two populations of *E. glaucus* (southern California versus northern California) exposed in a factorial experiment involving ozone, mycorrhizal inoculation with *Glomus intraradices* Schenck and Smith, and plant source population. Ozone had a subtle effect on leaf area and number of tillers but did not affect overall root:shoot ratio in either population. The impact of ozone on above-ground growth characteristics was most pronounced in the southern population that came from a high-ozone environment, while below-ground responses such as reduced arbuscular colonization was most pronounced in the northern population which originated in a low-ozone environment. Further analysis of soil characteristics from the northern population of plants revealed a significant reduction in active soil bacterial biomass and an increase in total fungi per gram dry weight soil, suggesting a possible role for ozone in altering soil processes. Whether or not population differences in response to ozone were due to genetic shifts resulting from prior ozone remains to be determined. However, these subtle but important differences in population response to ozone above- and below-ground have significant implications in any attempt to generalize plant response, even within a species. Future research efforts need to include better characterization of intraspecific variation in response to ozone as well as possible adaptive strategies that may result from chronic ozone exposure.