Seasonal Influences on Ozone Uptake and Foliar Injury to Ponderosa and Jeffrey Pines at a Southern California Site[1]

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Abstract

*Ambient ozone was monitored from 1992 to 1994 near a forested site dominated by mature Jeffrey and ponderosa pines (*Pinus jeffrey *Grev. & Balf. and* Pinus ponderosa *Dougl. ex Laws.) at 2,000 m in the San Bernardino Mountains of southern California. Ozone injury symptoms, including percent chlorotic mottle and foliage retention, were evaluated on 130 mature pines in September of 1991 to 1994 at a site 2 km from the ozone monitor. Symptom measurements were combined in an ozone injury index (OII) that represented the average crown condition of each plot. Leaf stomatal conductance and available soil water were measured biweekly from March to November at one of the plots from 1992 to 1994. Mean annual ozone concentrations were relatively constant for the 3 years. However, the distribution of individual trees in the 0 to 100 range of the OII showed a shift from 1991 to 1994 to higher frequencies of trees in classes representing greater amounts of injury. Compared with 1991, in 1993 and 1994 more trees remained in the higher injury classes. Maximum rates of stomatal conductance and maximum ozone uptake occurred in June of each year, but the total annual ozone flux varied as the amount of available soil water varied with seasonal precipitation. The period of April to June or May to July, depending upon year, accounted for 70 to 75 percent of annual ozone flux, confirming the high correlation observed between ambient ozone concentrations from April to June and development of chlorotic mottle on the needles. Foliar injury to current-year needles, which served as a marker of ozone response for a single exposure season, was greatest in 1992, coincident with higher flux of ozone to foliage in 1992, compared with 1993 and 1994. These data confirm that the period of maximum ozone impact on these pines is early in the growing season, and that ambient ozone after July had less effect on the development of foliar ozone injury on older pine needles. Year-to-year variation in ozone injury to pines was influenced both by the status of soil moisture availability in summer at this location and the internal foliar dynamics of the trees as they recovered from drought.*

Introduction

Annual precipitation throughout the ranges of ponderosa and Jeffrey pines (*Pinus ponderosa* Dougl. ex Laws. and *Pinus jeffreyi* Grev. & Balf.) in the mountains of California is subjected to strong seasonal influences, with more than 90 percent of total precipitation falling in the months of October to April. Annual precipitation totals are also highly variable, and the long-term annual mean is composed of many years with low total precipitation and a few years of much greater than average precipitation (NOAA 1995). Summer drought is the norm, interrupted by occasional brief, local thunderstorms. The growth cycles of the trees have become adapted to these highly variable conditions, and gas exchange in the pines closely followed patterns of soil water availability and vapor pressure deficit (Helms 1970, 1971).

Because the uptake of ozone by plants is controlled by stomatal conductance (Runeckles 1992), annual and seasonal patterns of ozone uptake in ponderosa and Jeffrey pines may also be mediated by environmental factors, such as soil water availability and vapor pressure deficit, that control gas exchange (Helms 1971). Intrinsic factors, such as leaf age (Helms 1970) and amount of foliar ozone injury (Coyne and Bingham 1982), also influence the rate of gas exchange in ponderosa pines. Those factors that influence stomatal conductance could also affect the response of the tree to ozone and could be used to model ozone uptake and foliar injury responses of trees in the field. Thus, measurements of stomatal conductance and calculations of ozone flux to leaves may be used to bridge the gap between measurements of ambient ozone concentrations in the forest and measurements of foliar injury symptoms on pines.

The objectives of this study were to measure seasonal ozone flux to the foliage of mature ponderosa and Jeffrey pines as influenced by environmental and physiological factors, and to correlate ozone flux with observed changes in ozone injury measured on mature pines at the same location in the San Bernardino Mountains of southern California.

[1] An abbreviated version of this paper was presented at the International Symposium on Air Pollution and Climate Change Effects on Forest Ecosystems, February 5-9, 1996, Riverside, California.

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Materials and Methods

Ambient Ozone Concentrations

Continuous measurements of ozone concentrations from January 1992 to December 1994 were obtained from a meteorological station located at Barton Flats at 2,000 m in the mixed conifer forest zone of the San Bernardino Mountains in southern California. Ozone air quality was measured with a certified Environmental Protection Agency (EPA)-equivalent ozone analyzer, calibrated and maintained according to standard air quality protocols (Miller and others 1996a). Precipitation data were obtained from a meteorological station located at Big Bear Lake, 10 km north of the site.

Pine Plot Evaluations

Ozone injury symptoms were evaluated each September from 1991 to 1994 on 5 branches of 130 mature ponderosa or Jeffrey pines located at an elevation of 2,000 to 2,200 m, 2 km from the meteorological station. The number of annual needle whorls was counted and each whorl was evaluated for percent of needle area with chlorotic mottle, percent of needles remaining in each whorl, and average needle length of each whorl. The percent live crown was determined as the proportion of the total crown with any live branches relative to the total tree height. These parameters were combined into an ozone injury index (OII) by weighting chlorotic mottle by 0.40, abscission by 0.40, needle length by 0.10, and percent live crown by 0.10 (Miller and others 1996b). Injury scores were averaged to obtain the average crown condition for each plot for each year. The distribution of trees in 10 unit increments of the 0 to 100 of the OII were also determined annually. Higher numerical values of the OII mean greater chronic injury.

Measurements of Stomatal Conductance

Leaf stomatal conductance was measured twice monthly from March to November and monthly from December to February of 1992 to 1994 at 25 m height in the canopy of a stand of mature ponderosa and Jeffrey pines on one of the pine evaluation plots. Access to the top of the trees was provided by a tower that penetrated through the canopy to a height of 30 m. Branches from three trees were accessible from the tower, and stomatal conductance measurements were taken on all available age classes of needles on three branches from each of three mature pines. Stomatal conductance was measured with a steady-state porometer (Model LI-1600, Licor Inc., Lincoln, NE)[3] equipped with a cuvette specifically designed for conifer foliage. Needle surface area was calculated by using the diameter length of the cuvette opening (5 cm) multiplied by the diameter of the needle fascicle and the number of needles in the fascicle (usually three). Fascicle diameter was measured with an electronic digital caliper (Mitutoyo Corp., Japan) to the nearest 0.01 mm. Measurements were taken usually between 0900 and 1300, when rates of stomatal conductance were at maximum. However, stomatal conductance measured hourly throughout three complete diurnal cycles showed that conductance rates in mature pines varied little during most of the daylight hours.[4] Photosynthetically active radiation, relative humidity, leaf and ambient temperature were measured simultaneously with conductance measurements by sensors on the porometer cuvette. Volumetric soil water was measured bi-weekly under the tree canopy, except during months with snow cover, using a time domain reflectometry instrument (TRASE Model 1010X, SoilMoisture Corp., Santa Barbara, CA) equipped with 15 cm soil probes.

Ozone Flux

Flux of ozone to pine foliage was calculated as:

$$\text{Flux } (O_3)(\mu\text{mol m}^{-2}\text{ d}^{-1}) = [O_3]_a\,(\mu\text{mol mol}^{-1}) \times g_s(O_3)\,(\text{mol m}^{-2}\text{ d}^{-1})$$

in which $[O_3]_a$ = ambient ozone concentration per day, averaged over the number

[3] Mention of trade names or products is for information only and does not imply endorsement by the U.S. Department of Agriculture.

[4] Unpublished data on file at the Pacific Southwest Research Station, Riverside, Calif.

of daylight hours from 30 min after sunrise to 30 min before sunset. Stomatal conductance to ozone ($g_s(O_3)$) was calculated from $g_s(H_2O)$ by multiplying by the ratio of the molecular weights of O_3 to H_2O. Boundary layer resistance in the well-mixed conifer cuvette was factory-set in the instrument at 0.07 s m^{-1}. The actual boundary layer resistance of the measured pine needles would depend upon wind speed, but generally at the upper layers of the canopy wind speed > 5 m s^{-1}. Other aspects of ozone transport from the atmosphere to internal leaf surfaces (Runeckles 1992) were ignored for the purposes of these calculations. Mean daily ozone flux (µg m^{-2} d^{-1}), averaged over each month, was calculated from mean monthly daylight ozone concentrations and mean daily rates of stomatal conductance for each month of the 3-year study.

Results and Discussion

Average ozone concentrations were relatively uniform at Barton Flats during the 3 years of the study. Mean monthly daylight ozone concentrations ranged from 38 parts per billion (ppb) in January to 83 ppb in June (*fig. 1*). Highest mean ozone concentrations occurred in June of 1992 and 1994, but ozone levels were lower in July and August of 1992 because of unusually cloudy and rainy conditions during the late summer of 1992. Ambient ozone averaged 18 percent lower in July 1992 relative to July 1994; but for the 5-month period from May to September, ozone concentrations averaged 73 ppb, 74 ppb, and 74 ppb for 1992, 1993, and 1994, respectively.

Annual precipitation totals were highly variable at the Barton Flats site (*fig. 2*). For the 4-year period preceding the study, precipitation totals averaged 50 percent below the long-term mean of 83 cm. This prolonged period of drought was reflected in the foliage of ponderosa and Jeffrey pines at the site, which were significantly shorter and lighter in weight than needles produced after the drought had been relieved in 1991 (Miller and others 1996a). More than 90 percent of annual total precipitation fell during December to March of each of the three years of the study (Miller and others 1996a).

This pattern of several years of drought before the study, followed by rapid recovery from drought stress beginning in 1991 was reflected in the amount of

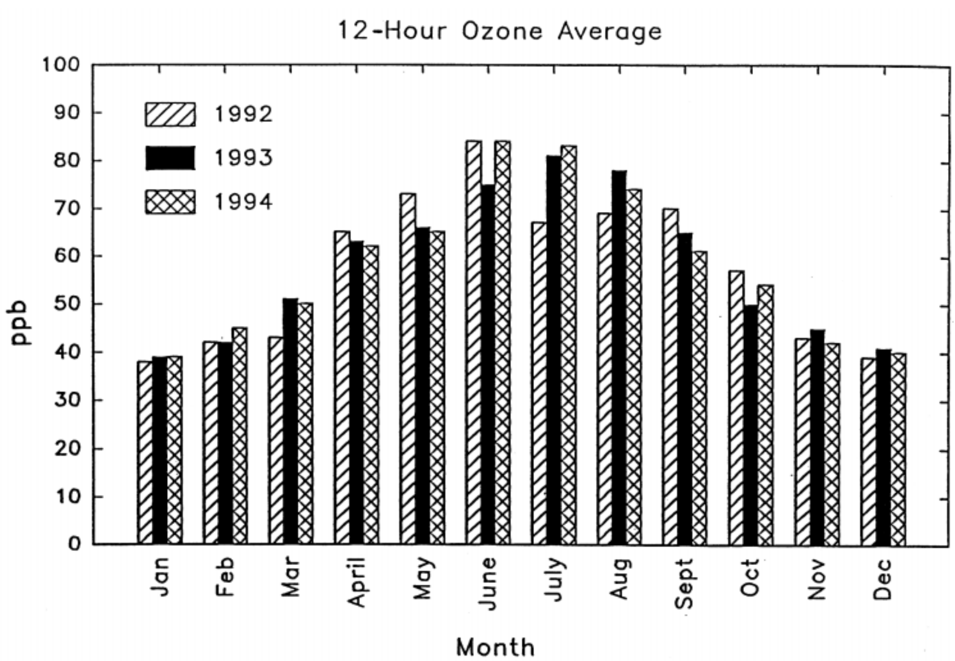


Figure 1 — Monthly 12-hour (0600-1800) ozone averages for Barton Flats, San Bernardino Mountains, California, 1992 to 1994.

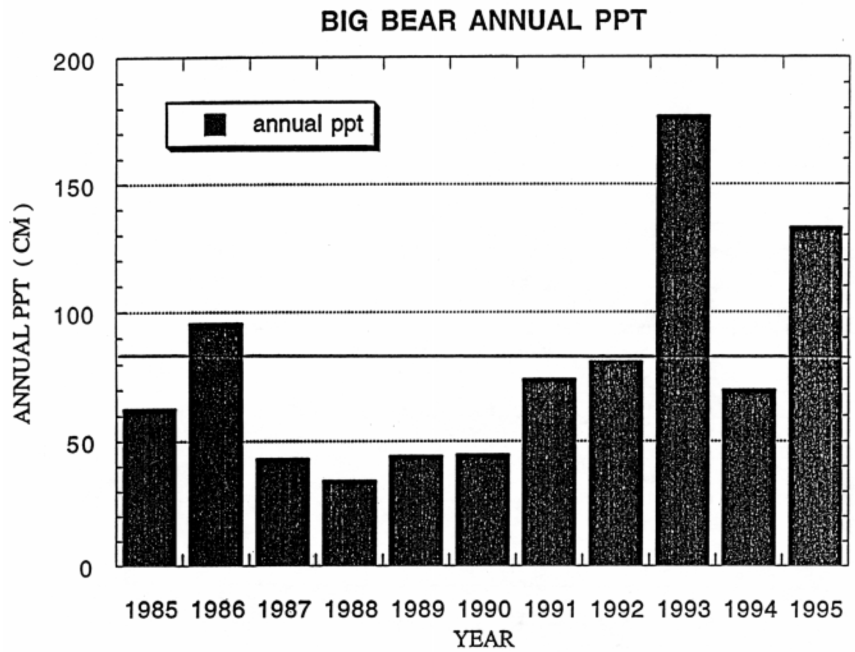


Figure 2 — Annual total precipitation at Big Bear Lake, San Bernardino Mountains, 10 km north of Barton Flats, 1985 to 1995.

ozone injury on the ponderosa and Jeffrey pines at Barton Flats (*table 1*). In 1991, the mature pines averaged more than 4 years of needle whorl retention and the ozone injury index (OII) averaged 38.3. By 1992, the number of age classes of needles had decreased to an average of 3.6 and the OII had increased significantly ($p < 0.001$) to 47.5, an increase of 24 percent. The OII stabilized over the next 2 years, but the number of needle whorls retained continued to decline (*table 1*), as the fascicles retained during the drought were replaced by larger, more physiologically-active needles.

Table 1 — *Ozone injury index (OII), percent chlorotic mottle (CM) on current-year needles, and number of age classes of needles retained on mature ponderosa and Jeffrey pines at Barton Flats, San Bernardino Mountains, recorded in September 1991 to1994.*[1]

Year	OII	CM (pct)	Age classes retained
1991	38.3	0.076	4.2
1992	47.5	0.798	3.6
1993	47.5	0.258	3.4
1994	49.2	0.005	3.3

[1] Data are means of 5 branches from 130 trees in 3 plots at the site.

Distribution curves of the frequency of trees in 10-unit classes of the OII (*fig. 3*) showed a shift from a relatively flat distribution in 1991 to clustering in the higher injury classes beginning in 1992 and continuing in 1993 and 1994. Injury on current-year needles in 1992 was 10 times greater than in 1991 and three times greater than in 1993. Injury on current-year needles was very low in the drought year of 1994 (*table 1*). The effect of drought in reducing the impact of ozone on these mature pines in the San Bernardino Mountains was comparable to the responses of drought-stressed ponderosa pine seedlings exposed to ozone under experimental conditions (Temple and others 1992).

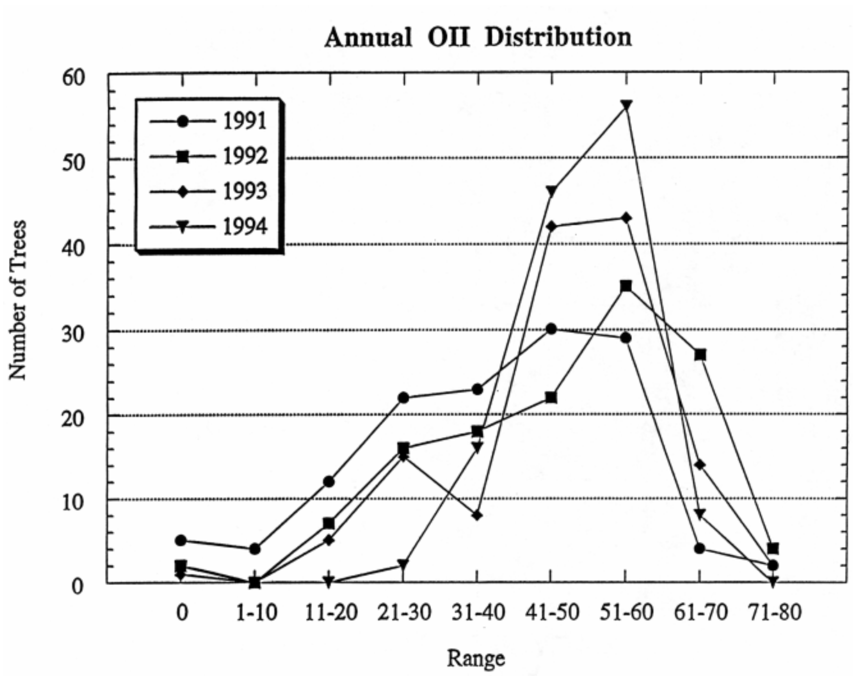


Figure 3 — Distribution of 130 ponderosa and Jeffrey pines in 10 unit classes of the ozone injury index (OII) from 1991 to 1994 (higher OII scores mean more injury).

Seasonal trends in rates of stomatal conductance of pine needles generally followed the same patterns in 1992 to 1994, although variations in total precipitation and summer rainfall patterns that influenced soil water retention altered conductance rates, particularly in mid- to late summer. In 1992, conductance in 1-year-old needles peaked in June and gradually declined (*fig. 4*), although conductance increased again in late August in response to summer rains that had increased soil water content 2 weeks earlier. Current needles showed measurable rates of gas exchange in July, but conductance rates in these needles remained low, relative to maximum rates of 1-year-old needles in June. In 1993, maximum conductance rates of 1-year-old needles peaked in early June, then gradually declined, except for small increases in July and September in response to increased soil water content 2 to 3

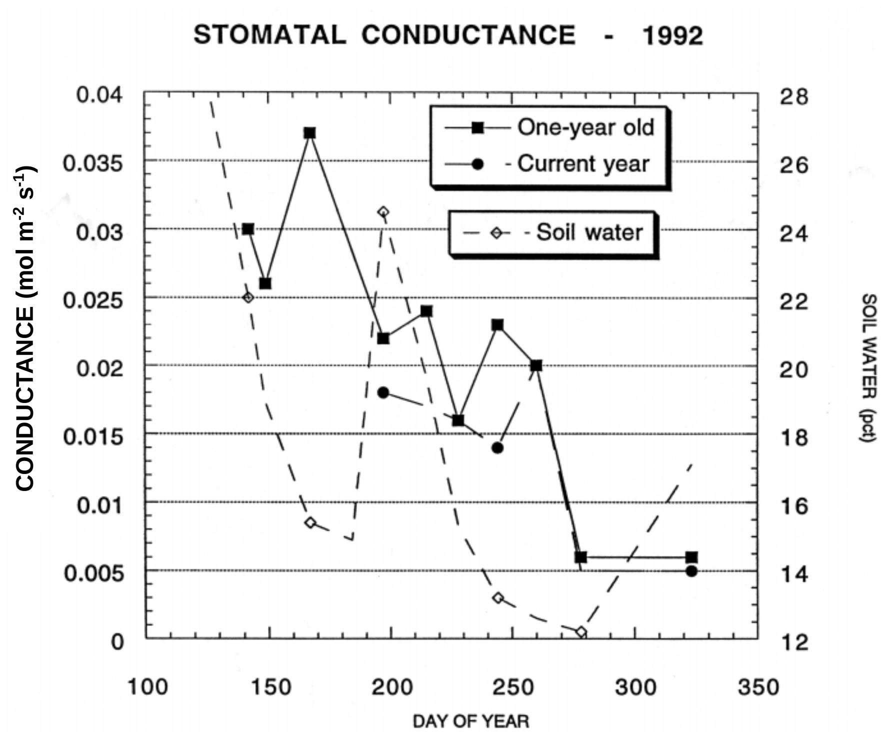
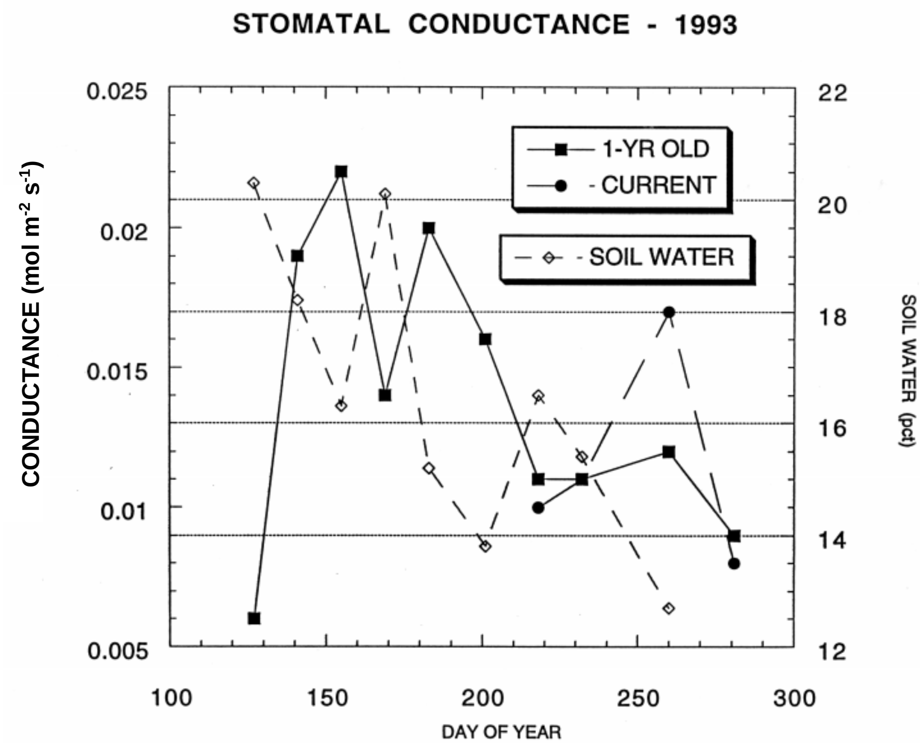


Figure 4 — Seasonal trends in maximum rates of stomatal conductance in 1-year-old needles of mature ponderosa and Jeffrey pines (n=3), and volumetric soil water content under the canopy at Barton Flats, San Bernardino Mountains, 1992.

weeks earlier (*fig. 5*). Current-year needles developed measurable conductance in mid-August, and conductance rates in current needles peaked in mid-September, but maximum conductance rates in current needles were below peak conductance rates in 1-year-old needles. In 1994, winter precipitation (1993-1994) was 30 percent below average, and soil water content depleted rapidly during the summer. Rates of stomatal conductance closely followed soil water content, with peak conductance in April and May, followed by rapid reductions in conductance as the soil dried during the summer (*fig. 6*). Current needles became active in early August, but conductance in current needles remained low for the rest of the year.

Figure 5 — Seasonal trends in maximum rates of stomatal conductance in 1-year-old needles of mature ponderosa and Jeffrey pines (n=3), and volumetric soil water content under the canopy at Barton Flats, San Bernardino Mountains, 1993.



These results are similar to those reported for ponderosa pine in the Sierra Nevada, where gas exchange in photosynthesis was influenced primarily by temperature and light intensity under favorable soil water conditions. In mid- to late summer, under high temperature and low soil water, photosynthetic rates declined in ponderosa pine in response to increased vapor pressure deficits (Helms 1970, 1971). However, reports of higher rates of gas exchange in Jeffrey pine during winter months compared with rates in September (Patterson and Rundel 1989) were *not* confirmed by these results

Highest mean daily ozone flux to 1-year-old needles of mature pines at Barton Flats for the study period was in 1992 (*fig. 7*), reflecting the high stomatal conductance rates measured in 1-year-old needles in 1992. The high rates of conductance in these 1991 needles in 1992 may have been due to the high rate of physiological activity in these needles, as previous years' needles produced during the drought years were significantly smaller than 1991 needles, and had already begun to senesce by 1992 (Miller and others 1996a). Ozone flux peaked in June, and this month accounted for 28 percent of the total yearly ozone flux in 1992. In 1993, ozone flux was more evenly distributed throughout the growing season, but total ozone flux averaged 40 percent less than in 1992. Flux rates were higher in 1994, although precipitation was lower than in 1993 (*fig. 2*). In response to rapid decreases in rates of conductance (*fig. 6*), ozone flux was higher in April 1994 but lower in July, August, and September than in 1992 and 1993. For the 3 years of the study, the months of April to July accounted for more than 60 percent of total annual ozone flux.

These results are consistent with statistical analyses of ambient ozone concentrations and development of ozone injury symptoms on pines, in which highest correlations were found between ozone injury and ozone concentrations between April 15 and July 15 (Miller and others 1996a).

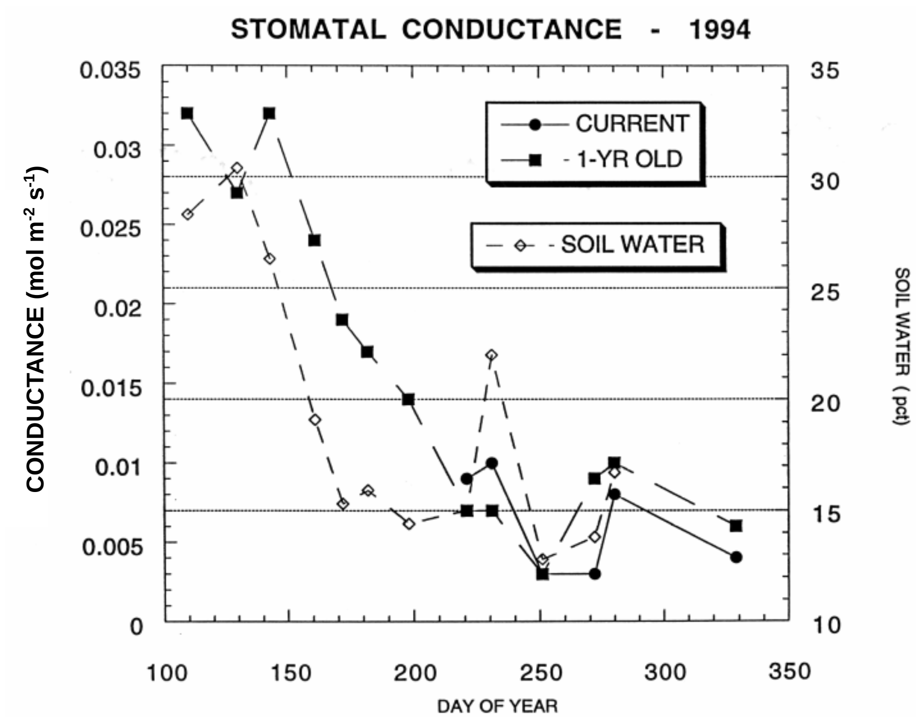


Figure 6 — Seasonal trends in maximum rates of stomatal conductance in 1-year-old needles of mature ponderosa and Jeffrey pines (n=3), and volumetric soil water content under the canopy at Barton Flats, San Bernardino Mountains, 1994.

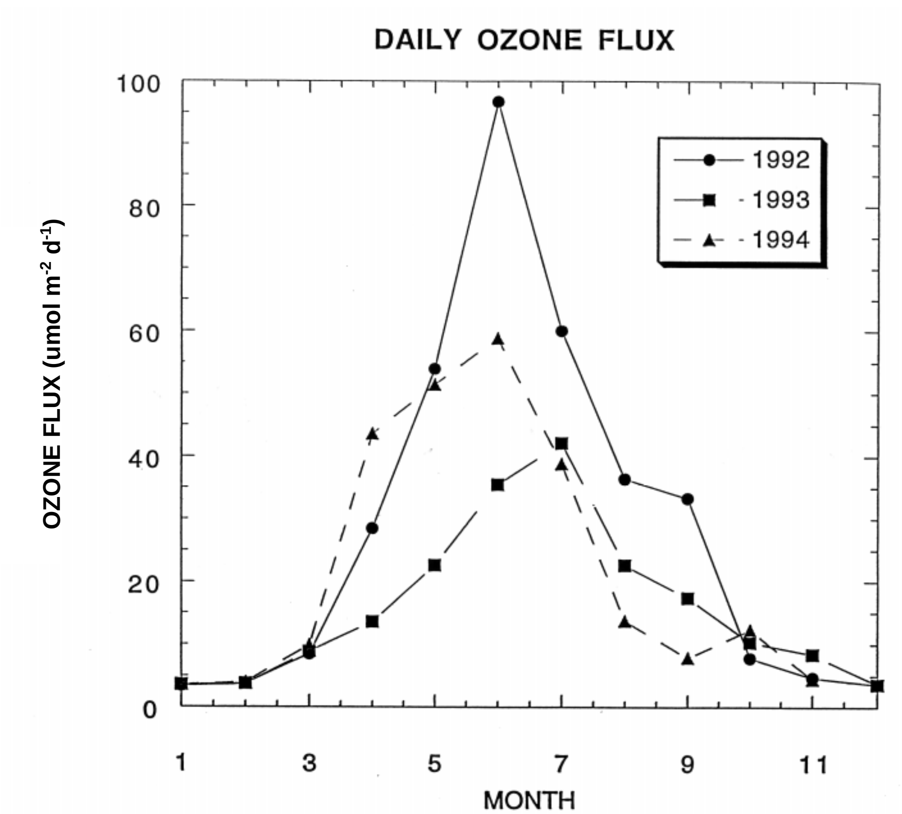


Figure 7 — Mean daily ozone flux to 1-year-old needles of mature ponderosa and Jeffrey pines at Barton Flats, San Bernardino Mountains, 1992 to 1994.

Conclusions

Results of this study of ozone injury development relative to stomatal conductance and ozone flux to foliage of mature ponderosa and Jeffrey pines in the San Bernardino Mountains showed that ozone injury increased substantially in the year following relief from a prolonged period of drought. The distribution of individual trees in OII classes showed a shift from 1991 to 1992 to greater numbers of trees in classes representing higher injury levels. Seasonal patterns of conductance followed trends of diminishing soil water as the summer progressed, and highest rates of ozone flux occured early in the growing season, with relatively little ozone flux after July. However, the high level of variability in annual precipitation influenced the size and persistence of annual needle whorls, particularly during and after recovery from a prolonged drought. These internal foliar dynamics interacted with external environmental parameters, such as winter precipitation and soil water depletion, to influence rates of stomatal conductance and ozone flux to pine foliage, which influenced development of ozone injury on these trees.

Acknowledgments

We thank Anthony Gomez and David Jones for technical support, and Susan Schilling and Delparde Guthrey for assistance with data analyses. We thank Laurie Dunn for technical editing of this manuscript. We also thank Brent Takemoto for his support of this project. This research was sponsored by the California Air Resources Board, Contract No. A032-180.

References

Coyne, Patrick I.; Bingham, Gail E. 1982. **Variation in photosynthesis and stomatal conductance in an ozone-stressed ponderosa pine stand: light response.** Forest Science **28: 257-273.**

Helms, John A. 1970**. Summer net photosynthesis of ponderosa pine in its natural environment.** Photosynthetica 4: 243-253.

Helms, John A. 1971**. Environmental control of net photosynthesis in naturally growing *Pinus ponderosa* Laws.** Ecology 53: 92-101**.**

Miller, Paul R.; Chow, Judy; Watson, John; Bytnerowicz, Andrzej; Fenn, Mark; Poth, **Mark;** Taylor, George. 1996a**. Assessment of acidic deposition and ozone effects on conifer forests in the San Bernardino Mountains. Final Report, Contract No. A032-180.** California Air Resources Board, Sacramento, CA**.**

Miller, Paul R.; Stolte, Kenneth W.; Duriscoe, Daniel; Pronos, John, technical coordinators. 1996b**. Evaluating ozone air pollution effects on pines in the western United States.** Gen. Tech. Rep. PSW-GTR-155. Albany, CA: USDA Forest Service; 79 p.

NOAA. 1995**. Climatological Atlas for California.** Washington, D.C.: National Oceanographic and Atmospheric Administration.

Patterson, Mark T.; Rundel, Philip W. 1989**. Seasonal physiological responses of ozone-stressed Jeffrey pine in Sequoia National Park, California.** In, Allen S., eds. Effects of air pollution on western forests. Pittsburgh, PA: Air and Waste Management Assoc.; 279-292.

Runeckles, Victor C. 1992**. Uptake of ozone by vegetation.** In: Lefohn, Allen S., ed. Surface level ozone exposures and their effects on vegetation. Chelsea, MI: Lewis Publ. Inc.; 157-188.

Temple, Patrick J.; Riechers, George H.; Miller, Paul R. 1992**. Foliar injury responses of ponderosa pine seedlings to ozone, wet and dry acidic deposition, and drought.** Environmental and Experimental Botany 32: 101-113.