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The effect of different atmospheric ozone partial pressures on photosynthesis and growth of nine fruit and nut tree species[1]

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Summary

Nursery stock of peach (*Prunus persica* L. Batsch, cv. O'Henry), nectarine (*P. persica* L. Batsch, cv. Fantasia), plum (*P. salicina* Lindel., cv. Casselman), apricot (*P. armeniaca* L., cv. Tilton), almond (*P. dulcis* Mill., cv. Nonpareil), prune (*P. domestica* L., cv. Improved French), cherry (*P. avium* L., cv. Bing), oriental pear (*Pyrus pyrifolia* Rehd., cv. 20th Century), and apple (*Malus pumula* Mill., cv. Granny Smith) were planted in open-top chambers on April 1, 1988 at the University of California's Kearney Agricultural Center located in the San Joaquin Valley (30°40′ N 119°40′ W). Trees were exposed to three atmospheric ozone partial pressures (charcoal-filtered air (C), ambient air (A), or ambient air + ozone (T)) from August 1 to November 17, 1988. The mean 12-h (0800 to 2000 h) ozone partial pressures measured in open-top chambers during the experimental period were 0.030, 0.051, and 0.117 $\mu Pa\ Pa^{-1}$ in the C, A and T treatments, respectively. Leaf net CO_2 assimilation rate decreased linearly with increasing 12-h mean ozone partial pressure for the almond, plum, apricot, prune, pear, and apple cultivars. Stomatal conductances of apricot, apple, almond, and plum decreased linearly with increasing ozone partial pressure. Cross-sectional area relative growth rates of almond, plum, apricot, and pear decreased linearly with increasing ozone partial pressure. Net CO_2 assimilation rate, stomatal conductance, and trunk growth of cherry, peach and nectarine were unaffected by the ozone treatments. Reduced leaf gas exchange probably contributed to ozone-induced growth reduction of the susceptible species and cultivars. Several of the commercial fruit tree species and cultivars studied were relatively tolerant to the ozone treatments.

Introduction

Chronic exposure to low partial pressures of ozone has a negative impact on growth of coniferous and deciduous tree species, which is apparently caused by an inhibitory effect of ozone on photosynthesis (Houston 1974, Townsend 1974, Steiner and Davis 1979, Reich 1983, Reich and Amundson 1985, Reich et al. 1987, Pye 1988). The rate of leaf photosynthesis is reduced when plants are exposed to low ozone partial pressures for an extended time (Reich 1983, Reich and Amundson 1985, Roper and Williams 1989), or when plants are exposed to an acute dose of the pollutant (Hill

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and Littlefield 1969, Roper and Williams 1989). Chronic exposure to low partial pressures of ozone may accelerate leaf aging and this may partially explain the decline in leaf photosynthetic capacity (Reich 1983).

Research on effects of ozone on the growth of woody perennials has been limited mostly to work with small, potted plants of forest tree species. These studies show that ambient ozone partial pressure can reduce dry matter production and growth (Steiner and Davis 1979, Reich and Amundson 1985, Taylor et al. 1986, Pye 1988). Ambient partial pressures of ozone have also been shown to reduce yields of field-grown *Vitis vinifera* relative to yields of plants grown in charcoal-filtered air (Brewer and Ashcroft 1983).

There has been no comprehensive study assessing the effects of ozone pollution on growth and photosynthesis of fruit and nut tree species. The objectives of this study were to determine the effects of ozone pollution on leaf net CO_2 assimilation and growth of nine fruit and nut tree species in the San Joaquin Valley of California. This fruit production region is characterized by ambient ozone partial pressures that consistently exceed U.S. Environmental Protection Agency standards of 0.12 μPa Pa^{-1} averaged over 1 hour (Cabrera et al. 1988). From August 1 to September 30 in 1983 and 1984 the peak hourly ozone partial pressures at the Kearney Agriculture Center exceeded the U.S. Environmental Protection Agency hourly standard 20 times (Brewer and Ashcroft 1985).

Materials and methods

Plant materials and ozone treatments

One-year-old trees (bud grafted the previous year) of peach (*Prunus persica* L. Batsch, cv. O'Henry), nectarine (*P. persica* L. Batsch, cv. Fantasia), plum (*P. salicina* Lindel. cv. Casselman), apricot (*P. armeniaca* L., cv. Tilton), almond (*P. dulcis* Mill., cv. Nonpareil), prune (*P. domestica* L., cv. Improved French), cherry (*P. avium* L., cv. Bing), oriental pear (*Pyrus pyrafolia* Rehd., cv. 20th Century), and apple (*Malus pumila*, cv. Granny Smith) were planted April 1, 1988 in 12 permanent open-top chambers at the University of California Kearney Agricultural Center near Fresno, California (30°40′ N 119°40′ W). Trees were on different rootstocks and had different trunk calipers at planting (Table 1). All trees were uniformly headed at planting to a height of 70 cm and one tree of each species was planted per chamber.

Cultural practices were the same as for commercial orchard establishment. Trees were flood irrigated approximately once a week throughout the growing season. Just before ozone exposure, each tree was fertilized with 45 g of ammonium nitrate.

Open-top chambers used in this study were igloo shaped with a 3.7 × 3.7 m square base and a circular, 3.1 m diameter open-top, 2.7 m above the chamber floor. Chamber frames were constructed of metal conduit with the walls consisting of 12 mil polyvinyl plastic. Air ducts within the chambers were two 20 cm and two 15 cm diameter PVC pipes that extended along the chamber floor from one side wall to the other (3.7 m long) equidistant from one another. Holes (5 × 13 cm) were cut in the

Table 1. Scientific, cultivar, and rootstock names, and caliper at planting of the nine tree species exposed to increased atmospheric ozone partial pressures.

Tree type	Scientific name	Cultivar	Rootstock	Caliper at planting (cm)
Peach	*Prunus persica* L. Batsch	O'Henry	Nemaguard	1.6
Plum	*P. salicina* Lindel.	Casselman	Citation	1.9
Apricot	*P. armeniaca* L.	Tilton	Myro	1.9
Almond	*P. dulcis* Mill.	Nonpareil	Nemaguard	1.6
Cherry	*P. avium* L.	Bing	Colt	3.8
Prune	*P. domestica* L.	Improved French	Myro	1.9
Nectarine	*P. persica* L. Batsch	Fantasia	Nemaguard	1.3
Pear	*Pyrus pyrafolia* Rehd.	20th Century	Betch	0.8
Apple	*Malus pumila* Mill.	Granny Smith	Emla III	1.6

PVC pipe 31 cm apart to permit air to flow upward into the chambers. Plastic walls were put on the chambers between July 20 and 24, 1988, and blowers were turned on at that time. Blowers provided approximately 67 m^3 min^{-1} air, enough to change the air volume in the chambers twice a minute, and were operated continuously.

Ozone treatments began on August 1 and continued until November 17, 1988, thereafter the chamber tops were removed. Trees were overwintered and then allowed to flush the following spring (1989). Trees were removed from the chambers April 1, 1989.

Ozone treatments were charcoal-filtered air (C), ambient air (A), and ambient air + ozone (T). Treatments were randomly assigned to chambers and there were four chambers (replicates) per treatment. Ozone partial pressures in the chambers were measured with a Dasibi Model 1003 AH Ozone Analyzer. Calibration occurred weekly and involved cleaning and frequency count checks. An Apple IIe microcomputer interfaced with Cyborg's Integrated System for Automated Acquisition and Control (Model 91A) permitted sequential sampling of chamber ozone partial pressure hourly from 0800 to 2000 h Pacific Daylight Time (PDT) daily. Chambers were connected to the monitoring system by teflon tubing and solenoid valves. Inlets for air samples were suspended 1 m above the soil in the center of each chamber. Air from each chamber was passed through the monitoring system for 2 min before measuring ozone partial pressures to permit residue purging from common sampling lines and the ozone monitor.

Ozone for the ambient air + ozone (T) treatment chambers was generated from ambient air with an OREC Model 038-AR/0 Ozone Generator and delivered by teflon tubing to the air stream of the chambers. The ozone generator was computer controlled to operate at full potential from 0800 to 2000 h. This resulted in ozone partial pressures approximately twice ambient.

Ozone 12-h means (0800–2000 h PDT) and the number of hours with ozone partial pressures greater than 0.10 μPa Pa^{-1} and 0.20 μPa Pa^{-1} were calculated for each treatment. These data were used in assessing ozone effects on tree growth and development.

Gas exchange

Approximately three weeks after treatments began, measurements of leaf net CO_2 assimilation and stomatal conductance were made on a single species each day. Excluding weekends and cloudy days, measurements were repeated at 16-day intervals and at the end of the study each species had been measured four times. Measurements were made on four leaves of every tree (16 leaves of each species per treatment, 48 leaves per sample day). These were fully expanded leaves in direct sunlight taken from a point just above the location of the last leaf to have fully expanded on August 1, 1988. Measurements were made between 1030 and 1130 h PDT when PAR was saturating and air temperature was optimal for photosynthesis.

All measurements were made with an Analytical Development Corporation (Hoddesdon, England) Portable Infrared CO_2 Analyzer (Model LCA-2), Air Supply Unit with Mass Flowmeter (Model ASUM), Data Processor for the LCA-2 (Model DL-2), and a broad leaf, Parkinson Leaf Chamber. The IRGA was used in the differential mode. Air for the leaf chamber was taken from the internal duct system of the open-top chamber in which the tree was growing.

Growth measurements

From August 1, 1988 (treatment initiation), and at 2-month intervals through December 1, 1988, the circumference of each tree trunk was measured with a tape. Painted bands on the trees just above the soil-line were used as reference points to minimize measurement errors. The increase in trunk cross-sectional area from August 1 to December 1, 1988 was calculated by means of the equation: cross-sectional area = $\text{circumference}^2/4\pi$.

Four growing branches per tree were selected on all species to follow branch growth and leaf number. Four branches of peach, apricot, cherry, nectarine, apple, pear, and almond were tagged on August 1 above the last fully expanded leaf, so that any increases in branch length and leaf number above this point could be determined. Branches on plum and prune were tagged and then summer pruned to prevent them from extending above the chamber top. The lateral branch that emerged immediately below the pruning cut was used for branch measurements.

In all nine species, branch length and leaf number determinations were made on August 16 and September 1 and 21, 1988, and January 10 and April 1, 1989. Because there were no leaves on the trees on January 10, counts of node numbers per branch were made instead of leaf number. Leaves of the trees were inspected for visible symptoms of chronic ozone injury when measurements were taken.

Statistical analysis

A factorial arrangement of three ozone partial pressures and nine species in a split-plot experimental design was replicated four times, with ozone partial pressure as the main plot. Data collected only once during the study were analyzed by a two-way ANOVA. Repeated measurements of photosynthesis and growth during the trial were analyzed by species in a split block design for ozone partial pressure and date effects. Significantly different species responses were detected at the first measurement date and remained apparent on each subsequent measurement date (data not shown). The primary purpose of the present study was not to develop dose-response relationships, but to examine the long-term chronic effects of increased atmospheric ozone partial pressures. As a consequence, because there were no ozone by date interactions, all measurement dates were averaged and average values for ozone partial pressures were analyzed as a split plot with species. Duncan's Multiple Range Test of the ozone partial pressure regression coefficients (slopes) for each species was used to separate significant partial pressure by species interactions.

Results

Ozone treatments

Hourly ozone partial pressures were averaged from August 1 to November 17, 1988 (Figure 1). The 12-h mean ozone partial pressure (0800 to 2000 h PDT) of the charcoal-filtered air (C) was 60% that of the ambient air (A), which was less than half that of the ambient air + ozone (T) (Table 2). The number of hours each treatment ozone partial pressure was above 0.10 and 0.20 μPa Pa^{-1} also indicated large treatment differences (Table 2).

Gas exchange

Leaf assimilation rates, averaged across the four measurement dates, for plum, apricot, prune, almond, apple, and pear trees grown in the A and T chambers were

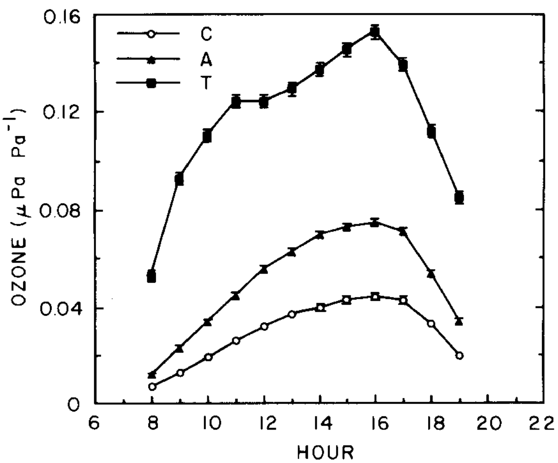

Figure 1. Average hourly ozone partial pressures from August 1 to November 17, 1988. Standard error bars are included when they are larger than the individual data symbol. C, A, and T refer to the charcoal-filtered, ambient, and ambient + ozone treatments, respectively.

significantly reduced when compared with those of trees in the C chambers (Table 3). Rates of CO_2 assimilation decreased linearly with increases in mean ozone partial pressure for almond, plum, apricot, prune, pear, and apple (Table 3, Figures 2a and 2b). However, assimilation rates of peach, nectarine, and cherry showed no significant response to increasing ozone partial pressure (Table 3, Figure 2c).

Stomatal conductances of plum, apricot, apple, and almond, averaged across the four dates, were significantly reduced in the A and T chambers compared with those of trees grown in the C chambers and the reduction with increasing ozone partial pressure was linear (Table 4, Figures 3a and 3b). Stomatal conductances of peach, nectarine, cherry, prune, and pear showed no significant response to increasing ozone partial pressure (Table 4, Figures 3b and 3c).

Tree growth

Cross-sectional area relative growth rates (RGR) for almond, plum, apricot, and pear

Table 2. Treatment 12-hour (0800–2000 h PDT) mean ozone partial pressures and the number of hours greater than 0.1 and 0.2 μPa Pa^{-1} for the experimental period from August 1 to November 17, 1988.

Treatment[1]	12-h Mean	Hours	
		>0.1 μPa Pa^{-1}	>0.2 μPa Pa^{-1}
	μPa Pa^{-1}		
C	0.030	0	0
A	0.051	33	0
T	0.117	761	127

[1] C, A, and T refer to the charcoal-filtered, ambient, and ambient + ozone treatments, respectively.

Table 3. Mean rate of leaf net CO_2 assimilation (μmol m^{-2} s^{-1}) and regression equations describing the relationships between leaf net CO_2 assimilation and increasing ozone partial pressure represented in Figures 2a–c.

	Leaf net CO_2 assimilation			Linear regression equation	Adjusted r^2	$P>F_{0.05}$
	C[1]	A	T			
Almond	23.10	22.70	11.60	$y = 28.4 - 140.8x$ (a)	0.85	*
Plum	13.87	12.75	7.37	$y = 16.5 - 77.2x$ (b)	0.78	*
Apricot	12.71	11.69	6.77	$y = 15.0 - 69.8x$ (b)	0.73	*
Prune	16.14	13.17	9.47	$y = 17.7 - 71.7x$ (b)	0.68	*
Pear	12.87	10.86	5.49	$y = 15.3 - 84.0x$ (b)	0.77	*
Apple	14.37	14.42	9.12	$y = 16.9 - 65.1x$ (b)	0.35	*
Peach	14.08	13.00	13.36	$y = 13.8 - 5.0x$ (c)	−0.07	NS
Nectarine	16.97	16.25	16.16	$y = 16.9 - 7.4x$ (c)	−0.05	NS
Cherry	11.20	11.67	10.29	$y = 0.40 - 0.32x$ (c)	−0.009	NS

[1] C, A, and T refer to the charcoal-filtered, ambient, and ambient + ozone treatments, respectively.
[2] Regression equations followed by a different letter in parenthesis indicate that the regression coefficients are significantly different ($P < 0.05$, $n = 12$) according to Duncan's Multiple Range Test of regression coefficients.

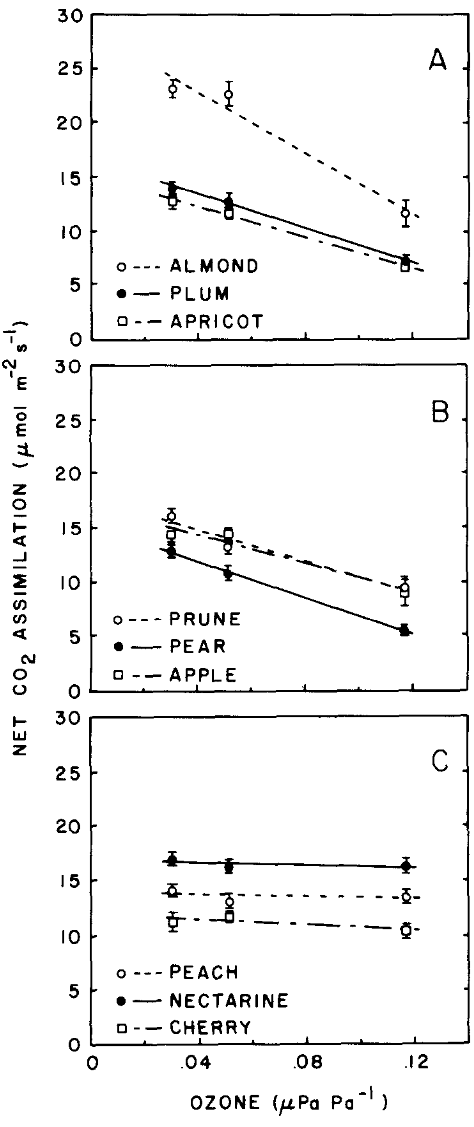

Figure 2. Relationship between leaf net CO_2 assimilation and ozone partial pressure. Bars represent ± one standard error. Regression equations for each species can be found in Table 3.

were significantly reduced in the A and T chambers relative to those of trees in the C chambers and the reduction with increasing 12-h mean ozone partial pressure was linear (Table 5, Figures 4a and 4b). Peach, nectarine, cherry, apple, and prune cross-sectional area RGRs were not significantly reduced with increasing ozone partial pressures (Table 5, Figures 4b and 4c).

Although shoot growth continued throughout the entire treatment period, increased ozone in the chamber atmosphere had no statistically significant effects on

Table 4. Mean rates of stomatal conductance (μmol H_2O m^{-2} s^{-1}) and regression equations describing the relationships between stomatal conductance and increasing ozone partial pressure represented in Figures 3a–c.[1]

	Stomatal conductance			Linear regression equation	Adjusted r^2	$P>F_{0.05}$
	C	A	T			
Almond	1.33	1.33	0.65	$y = 1.70 - 8.4x$ (a)	0.40	*
Plum	0.48	0.45	0.23	$y = 0.58 - 3.0x$ (b)	0.60	*
Apricot	0.40	0.37	0.24	$y = 0.46 - 1.9x$ (bc)	0.43	*
Prune	0.58	0.43	0.33	$y = 0.61 - 2.5x$ (b)	0.25	NS
Pear	0.47	0.38	0.41	$y = 0.45 - 0.4x$ (c)	−0.08	NS
Apple	0.61	0.58	0.34	$y = 0.72 - 3.2x$ (b)	0.77	*
Peach	0.53	0.43	0.46	$y = 0.51 - 0.5x$ (c)	−0.02	NS
Nectarine	0.53	0.50	0.48	$y = 0.54 - 0.5x$ (c)	−0.03	NS
Cherry	0.38	0.40	0.36	$y = 0.40 - 0.3x$ (c)	−0.09	NS

[1] Other information as found in Table 3.

shoot or branch length or leaf number (data not shown).

Foliar injury

Visible foliar injury in several species was seen in the high ozone chambers approximately 3 weeks after treatment began. Throughout the study, no leaf injury was seen on any species in the C and A treatments. Initially, visible injury in the T chambers consisted of chlorotic spots and yellow flecking on the leaf surfaces of older foliage. This foliage had developed on the trees in the ambient environment before treatment began. Over time, these chlorotic areas became larger and turned brown due to tissue necrosis. Visible symptoms also began to appear on foliage that had emerged in the T atmosphere and were the same whether foliage developed before or during treatment. Symptoms were most noticeable on the almond trees and to a lesser extent on the plum, apricot, prune, and pear trees. No visible injury symptoms appeared on the peach, cherry, nectarine, or apple cultivars.

Soon after visible injury became evident in the T chambers, the lower leaves abscised. By the time the ozone monitoring period was completed (November 17, 1988), almond, apricot, and pear appeared to have lost approximately half of their older foliage. The plum and prune trees had lost about a quarter of their foliage, but the peach, cherry, nectarine, and apple trees had lost virtually no leaves. The majority of foliage that was lost had developed before treatment initiation and was therefore not included in the leaf number counts.

Discussion

Mean CO_2 assimilation rates of plum, apricot, almond, prune, apple, and pear were lower in air with ambient and twice ambient ozone partial pressures than in charcoal-filtered air. The reductions in net CO_2 assimilation due to ambient ozone partial

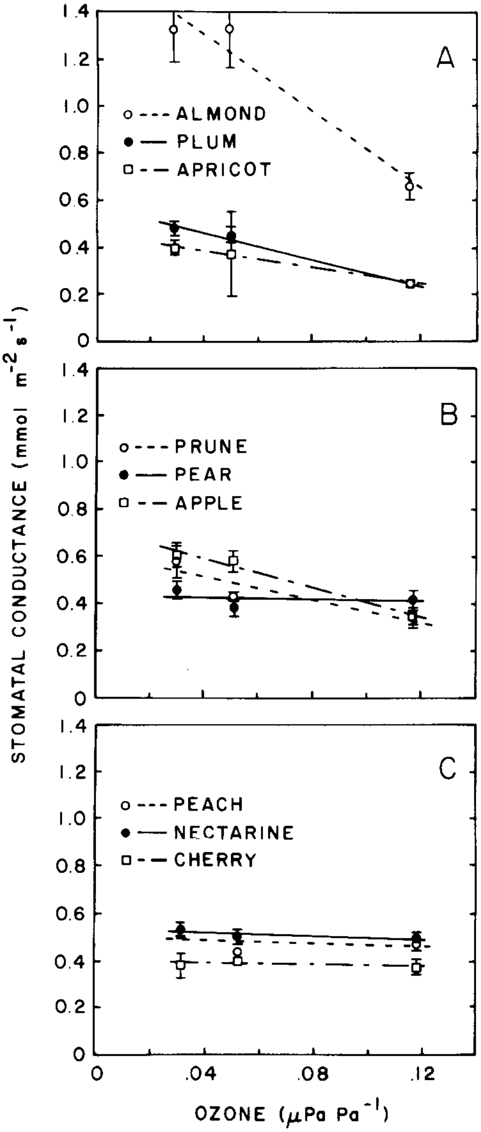

Figure 3. Relationship between stomatal conductance and ozone partial pressure. Bars represent ± one standard error. Regression equations for each species can be found in Table 4.

pressures exhibited by the trees in this study are similar to those reported by Reich and Amundson (1985) and Roper and Williams (1989). Data from 25 experiments on seedlings of 43 tree species also indicate that ozone can reduce photosynthesis at ambient partial pressures that are common in many areas (Pye 1988). Further, the reductions in net CO_2 assimilation for five of the species in the present study (plum, apricot, almond, apple, and pear) were linearly related to ozone partial pressure. Species with the greatest proportional decreases in photosynthesis also tended to

Table 5. Cross-sectional area relative growth rate ($cm^2\ cm^{-2}\ day^{-1} \times 1000$) and regression equations describing the relationships between cross-sectional area relative growth rate × 1000 and increasing atmospheric ozone partial pressure represented in Figures 4a–c.[1]

	Cross-sectional area RGR			Linear regression equation	Adjusted	$P>F_{0.1}$
	C	A	T		r^2	
Almond	6.7	6.3	4.8	$y = 7.4 - 22.1x$ (abc)	0.38	*
Plum	4.9	4.0	2.8	$y = 5.3 - 22.3x$ (abc)	0.36	*
Apricot	5.1	6.4	2.4	$y = 7.2 - 38.1x$ (a)	0.38	*
Prune	6.7	5.0	6.4	$y = 5.9 + 2.5x$ (de)	−0.10	NS
Pear	3.7	3.4	1.5	$y = 4.6 - 26.1x$ (ab)	0.42	*
Apple	3.9	3.1	2.6	$y = 4.1 - 13.2x$ (bc)	0.10	NS
Peach	9.0	8.2	9.5	$y = 8.3 + 9.1x$ (e)	0.09	NS
Nectarine	8.3	8.8	9.5	$y = 8.0 + 13.0x$ (e)	0.05	NS
Cherry	4.5	3.6	3.4	$y = 4.5 - 10.3x$ (cd)	−0.02	NS

[1] Other information as found in Table 3.

have the largest proportional reductions in growth, except for prune. Reich and Amundson (1985) also found that long-term exposure to ozone resulted in linear reductions in photosynthesis of sugar maple (*Acer saccharum*), white pine (*Pinus strobus*), hybrid poplar (*Populus deltoides* × *trichocarpa*), and red oak (*Quercus rubra*). The linear responses of net CO_2 assimilation to ozone partial pressure should simplify modeling the effects of air pollution on carbon assimilation by trees.

Increased ozone partial pressure did not inhibit photosynthesis in peach, nectarine, and cherry. Relative insensitivity of photosynthesis to ozone has also been reported in red spruce (*Picea rubens*) seedlings grown for 3 months at different ozone partial pressures (Laurence et al. 1989).

Stomatal conductance of plum, apricot, apple, and almond was lower in air with ambient and twice ambient ozone partial pressures than in charcoal-filtered air, which suggests that inhibition of assimilation by ozone in these species is a consequence, at least in part, of reduced diffusion of CO_2 to photosynthetic sites. However, increased ozone partial pressure did not reduce stomatal conductance of prune and pear, although it reduced net assimilation rates in these species. Lehnherr et al. (1988) concluded that, in spring wheat, (*Triticum aestivum*), reduced stomatal conductance with increasing ozone partial pressure was insufficient to account for the simultaneous reduction in photosynthesis. Additional research under steady state conditions will be necessary to explain whether changing stomatal conductance with increasing ozone partial pressure is responsible for the decrease in leaf net CO_2 assimilation of fruit and nut trees.

Of the aboveground growth measures, cross-sectional area RGR was the only one affected by ozone. There may, however, be more general effects of ozone on belowground growth, which is reported to be more sensitive to ozone than aboveground growth (Pye 1988).

Cross-sectional area RGRs decreased linearly in plum, apricot, almond, and pear.

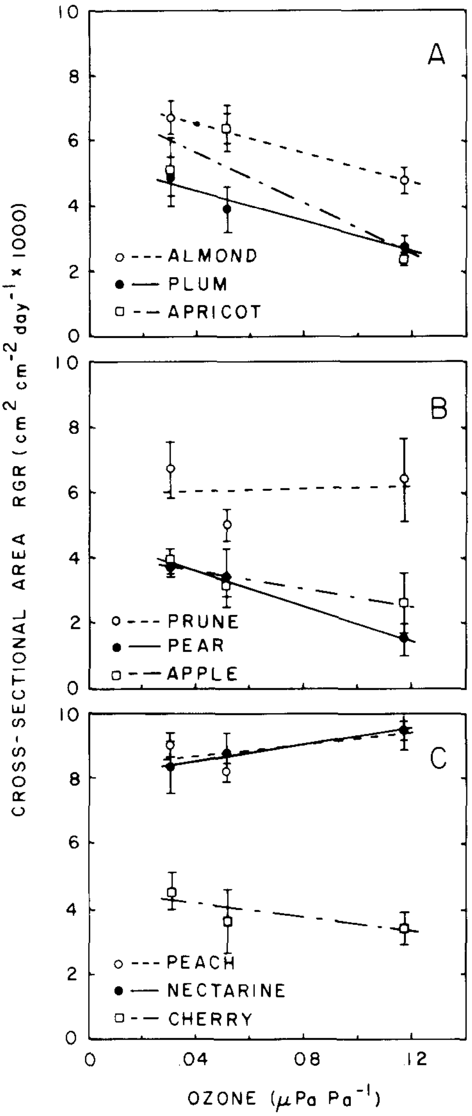

Figure 4. Relationship between cross-sectional area relative growth rate and ozone partial pressure. Bars represent ± one standard error. Regression equations for each species can be found in Table 5.

Adams et al. (1988) found significant differences in aboveground volume of loblolly pine (*Pinus taeda*) seedlings exposed to elevated ozone partial pressures. Decreases in trunk growth in the present study are apparently related to the decreases in photosynthesis. The absence of an ozone-induced reduction in cross-sectional area RGR of the peach, nectarine, cherry, and prune varieties reflects the absence of an effect of ozone on net assimilation rate in these plants. Similarly in red spruce neither photosynthesis, nor growth, were affected by a range of atmospheric ozone partial pressures (Taylor et al. 1986, Laurence et al. 1989).

Numerous *Pinus* and *Quercus* species have been found to be sensitive, tolerant, or of intermediate sensitivity to ozone (Davis and Gerhold 1976). Chappelka et al. (1988) reported different effects of increased atmospheric ozone on visible injury, shoot elongation, and biomass allocation in green ash (*Fraxinus pennsylvanica*) and white ash (*F. americana*). In both species, however, biomass accumulation decreased with increased atmospheric ozone partial pressures.

The present study demonstrates differences in ozone response among species of the genus *Prunus*. Ozone inhibited net assimiation in almond, plum, prune and apricot, but not in peach, nectarine, and cherry.

Cross-sectional area RGR in plum, almond, apricot, and pear trees decreased with increasing atmospheric ozone partial pressure. The growth reduction caused by ambient ozone partial pressures were small. However, as indicated by Reich and Amundson (1985), a 1 to 2% annual reduction in growth would result in a substantial reduction in total biomass after one or two decades. Therefore, the effect of small reductions in growth may be compounded over time. The maximum age of fruit orchards may be as great as 20 years, whereas orchards of nut crops, such as almonds, can be greater than 30 years. Thus, there is a distinct possibility that ambient partial pressures of ozone in the San Joaquin Valley of California will have a significant negative effect on fruit and nut tree growth, development, and productivity. However, the lack of effects of chronic ozone exposure on some of the species indicates that it may be possible to breed and select fruit and nut tree cultivars with increased resistance to ozone pollution.

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