The Effect of Ozone on Photosynthesis, Vegetative Growth and Productivity of Plum Trees (Prunus salicina, cv. "Casselman") in the San Joaquin Valley of California

Final Report

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ABSTRACT

Nursery stock of plum (Prunus salicina Lindel., cv. "Casselman") were planted 1 April 1988 in an experimental orchard at the University of California Kearney Agricultural Center near Fresno, California. The trees were enclosed in open-top fumigation chambers on 1 May 1989, and were exposed to three different ozone concentration treatments (charcoal filtered air, ambient air, and ambient air + ozone) during the 1989 through 1992 growing seasons (typically 1 April to 1 November). A no-chamber treatment plot was utilized to assess chamber effects on tree performance. This final report details the results of the exposures during the initial commercial bearing period (1991 through 1993) in this orchard. The mean 12-h (0800-2000 h Pacific Daylight Time [PDT]) ozone concentrations during the experimental periods in the charcoal filtered, ambient, ambient + ozone, and no-chamber treatments were 0.034, 0.050, 0.0945, and 0.058 ppm in 1991, and 0.027, 0.045, 0.087, and 0.054 ppm in 1992, respectively. Leaf net CO_2 assimilation rate of "Casselman" plum decreased with increasing ozone concentrations from the charcoal filtered to ambient + ozone treatment. There was no difference in plum leaf net CO_2 assimilation rate between the ambient chamber and no-chamber plots. Trees in the ambient + ozone treatment generally had greater leaf-fall earlier in the growing season than those of the other treatments. Trunk cross-sectional area growth was increased by increased ozone concentration in 1992. Fruit number per tree decreased as ozone concentration increased from the charcoal filtered to ambient + ozone treatment, significantly affecting yield. Yield of plum trees was 19.8, 15.9, 6.8, and 15.8 kg tree^{-1} in 1991, and 27.4, 23.7, 20.5, and 19.9 kg tree^{-1} in 1992 in the charcoal filtered, ambient, ambient + ozone, and no-chamber treatments, respectively.

The last year of the study determined possible carryover effects of the previous year's ozone environment on the current season's yield of trees grown under ambient conditions. Four of five treatment plots (redesignated as the post-chamber (PC) treatments;) were not enclosed or exposed to different ozone concentrations during the 1993 growing season. The mean 12-h (0800-2000 h PDT) ozone concentrations in 1993 in the exposed, charcoal filtered, ambient, ambient + ozone, and no-chamber treatments were 0.036, 0.047, 0.105, and 0.055 ppm respectively. The mean 12-h ozone concentration in the PC treatment was 0.052 ppm. Yield of plum trees exposed to the different ozone treatments in 1993 was 19.1, 14.5, 8.8, and 20.1 kg tree^{-1} for the charcoal filtered, ambient, and ambient + ozone, and no-chamber treatments, respectively. Yield of trees in the post-chamber treatments in 1993 (previously exposed to different ozone concentrations from 1989 through 1992) was 16.7, 17.9, and 16.0 kg tree^{-1} in the previous charcoal filtered, ambient, and ambient + ozone treatments, respectively. The similarity in yield of the post-chamber treatments indicates that a decrease or increase in air quality in the current growing season can affect yield of "Casselman" plum trees. The results indicate that the previous year's seasonal ozone concentration will affect the number of flowers formed for next season's crop and the current year's exposure to ozone will affect fruit abscission after fruit set. The exact mechanisms leading to reduced fruit numbers due to ozone exposure remain to be determined.

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DISCLAIMER STATEMENT

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SUMMARY AND CONCLUSIONS

Chronic exposure to low concentrations of ozone has been shown to have a negative effect on growth and photosynthesis of deciduous tree species. However, there has been no comprehensive study assessing the effects of ozone pollution on photosynthesis, vegetative growth, and productivity of fruit tree species. The objectives of the present contract were to determine the effects of ozone pollution on leaf net CO_2 assimilation, vegetative growth, and productivity of plum (Prunus salicina cv. "Casselman") during orchard development and full production in the San Joaquin Valley of California.

1. Data from this study indicate that ambient and 1.9 times ambient ozone concentrations reduced leaf net CO_2 assimilation of "Casselman" plum trees compared to rates of trees grown in charcoal filtered air.

2. Mean daily ozone concentrations greater than 0.09 ppm caused premature leaf-fall of these plum trees.

3. Increased ozone concentrations (ambient and 1.9 times ambient) significantly reduced yield compared to the trees grown in the charcoal filtered chambers. Yield of plum trees exposed to mean daily ozone concentrations greater than 0.09 ppm (the AO treatment) was reduced by 65% in 1991 (compared to trees in charcoal filtered air), by 25% in 1992, and 54% in 1993. The reductions in yield due to increased seasonal ozone concentrations were due to several factors. Higher concentrations of ozone generally reduced total number of flowers per tree counted each spring at bloom. However, 1992 was the only year in which there was a significant reduction. This would indicate that the previous year's ozone exposure may affect differentiation of the flower buds and possibly the number of flowers that set in the current season. The number of fruit that abscised from the tree prior to harvest was probably affected by both the current season's ozone exposure and also the number of fruit that set on each tree. It is unknown whether a reduction in seasonal carbohydrate production due to a reduction in net photosynthesis and increased leaf abscission of trees grown in higher ozone concentrations was responsible for observed differences in total flowers per tree, percent set and fruit abscission.

4. The ozone concentration was reduced approximately 14% in the ambient chambers compared to the no-chamber plots in the present study, but there were no leaf photosynthesis or yield differences between the two plots. It appears that the open-top chambers had little effect on the overall physiology, growth, and yield of "Casselman" plum trees and that results from this study could be extrapolated to trees of similar age growing under true orchard conditions.

5. Yield of plum trees exposed to different atmospheric ozone concentrations in 1993 was 19.1, 14.5, 8.8, and 20.1 kg $tree^{-1}$ in the charcoal filtered, ambient, ambient + ozone, and no-chamber treatments, respectively. However, yield of plum trees previously exposed to these ozone treatments from 1989 to 1992, but not exposed in 1993, was 16.7, 17.9, and 16.0, in

charcoal, ambient, and ambient + ozone treatment plots, kg tree^{-1}, respectively. The decrease in yield in the treatment plots previously exposed to charcoal filtered air (reduced ozone concentration) confirms that a decrease in air quality (to current ambient conditions) can reduce yield of "Casselman" plum trees. Conversely, the increase in yield in the treatment plots previously exposed to ambient + ozone (average 1.9 times current ambient ozone concentration from 1989 through 1992) indicates that an improvement in air quality could increase yield of "Casselman" plum trees.

6. A tree photosynthesis/carbon allocation model successfully predicted the effect of ozone on tree productivity. The fresh weights of individual fruits and final yield were predicted to within one standard error for charcoal filtered and ambient plus ozone treatments for all year/treatment combinations except charcoal filtered in 1992. Because ozone appears to reduce fruit number, the demand of carbon for fruit growth was lower in the ozone-treated trees. In the simulations, the reductions in carbon assimilation caused by ozone were less than the reduction in carbon demand for fruit growth. For this reason, fruit size was not reduced by ozone. The model does not make predictions about flower bud development for the subsequent year. We have insufficient information to determine whether the reduction in cumulative carbon assimilation would reduce bud number.

7. The extrapolation of the effects of ozone on "Casselman" plum productivity to other stone fruits is dependent upon several factors. Predominate among them would be the specific mode of action of ozone on reducing yield. Our results indicate the reduction in flowers per tree, reduced set, and increased fruit abscission due to increased ozone concentrations may be; 1) an indirect one by which a reduction in carbohydrate production (due to lower photosynthesis) affects fruit bud differentiation or 2) a direct effect of ozone diffusing through the bud's scales and disrupting cell differentiation. If carbohydrate production is the key element then tree species or cultivars that are tolerant to ozone with regard to photosynthesis may be unaffected. We have identified several species and cultivars that are tolerant of ozone (Retzlaff et al., 1991, 1992a). Conversely, if ozone has a direct effect on flower bud differentiation, trees that are tolerant (with regard to photosynthesis) to ozone, may still have a reduction in yield due to less fruit per tree. Another important factor would be date of fruit maturity (harvest). Different types of fruit trees and cultivars will ripen their fruit at different times (from early May through the end of August). We chose "Casselman" plum since it is a late maturing cultivar. Therefore, late maturing cultivars may be more susceptible to summer ozone pollution than early maturing cultivars.

RECOMMENDATIONS

1. Further examination of the ozone induced reductions in growth, and yield are necessary to more fully understand the potential impact of worsening air quality on San Joaquin Valley fruit and nut tree crop production.

2. It is not clear whether there is a direct affect of ozone fumigation on fruit bud differentiation, percent set and fruit abscission or an indirect one due to lack of carbohydrates. Counts of flower buds and fruit set are needed in order to quantify this reduced fruit number response.

3. A study should be commissioned to determine the feasibility of using branch chamber fumigation systems. This would allow further study on various other fruit and nut tree species that are too large to be grown in open-top fumigation chambers. This approach may also help establish whether ozone has a direct effect on fruit bud differentiation.

4. Air quality in the San Joaquin Valley of California should be improved to allow for maximum photosynthesis, growth, and yield of deciduous fruit and nut tree crops. An improvement in air quality would immediately improve tree productivity.

INTRODUCTION

The planting of an orchard is a long-term investment, usually taking three or more years to bear a commercial crop with continued economic production for another 15 to 30 years (LaRue and Johnson, 1989). The establishment and first few year's growth of newly planted trees are critical in determining overall orchard productivity once the trees are mature. It is during this time that the canopy and permanent limbs are established and the root system develops. Cultural practices have been developed to optimize growth during the establishment period (LaRue and Johnson, 1989). However, stress during this time could delay or disrupt orchard development with long-term orchard productivity being less than optimum. For example, apple trees were smaller and lower yielding as a result of competition for water and mineral nutrients during the first three years of growth in an orchard plot with a continuous grass cover compared to a clean-cultivated plot (Stinchcombe and Stott, 1983).

More than two million metric tons of fruit and nut crops are produced in the San Joaquin Valley of California annually. However, this fruit production region is characterized by ambient ozone concentrations that consistently exceed U. S. Environmental Protection Agency standards of 0.12 ppm at various times during the growing season (Cabrera et al., 1988). Ozone-induced reductions in photosynthesis previously have been related to reductions in crop growth and yield (Reich and Amundson, 1985; Lehnherr et al., 1988; Takemoto et al., 1988). Yield reductions in 'Valencia' orange trees have been documented in ozone concentrations greater than 0.020 ppm (Olszyk et al., 1990). Ozone induced yield reductions in other annual and perennial crops have been reported (Brewer and Ashcroft, 1983; Adaros et al., 1990; Mebrahtu et al., 1991).

Two studies have demonstrated that net photosynthesis and trunk circumference of various fruit and nut tree species and cultivars of the same species decreased with increasing ozone concentration (Retzlaff et al., 1991; Retzlaff et al., 1992a). However, these studies were conducted on nursery stock trees (bud grafted the previous year) which had been transplanted directly into open-top chambers. Retzlaff et al. (1992b) reported that increased ozone concentrations decreased yield of "Casselman" plum trees during the orchard establishment period. The effects of ozone air pollution on deciduous fruit tree crops in a production orchard following the orchard establishment period are unknown. A long-term study examining the effects of ozone on growth and productivity of plum trees grown in the San Joaquin Valley of California was established in 1988. This report describes the effects of different ozone concentrations during the fourth, fifth, and sixth years of tree growth, the first, second, and third commercial bearing years of this orchard. In addition, we determined possible carry over effects of the previous years' ozone environment on the current season's yield.

The final aspect of this study was to determine if a model to simulate reproductive and vegetative growth in peach trees (Grossman and DeJong, 1994b) could be adapted to plum trees used in this study. PEACH is a state-variable model in which fruit, leaf, current-year stem, branch, trunk and root weight are the state variables, and minimum and maximum air and soil temperatures, degree-days and solar radiation are the driving variables (see Figure 1 for schematic). The rate variables that characterize carbohydrate assimilation and utilization are derived from previous studies on photosynthesis, respiration and growth potential in peach trees (DeJong and Goudriaan 1989, DeJong et al. 1990, Grossman 1993, Grossman and DeJong 1994a). The model assumes that the trees are optimally irrigated and fertilized. The effect of ozone was incorporated into the model via ozone's effect on leaf photosynthesis.

MATERIALS AND METHODS

Plant Materials and Ozone Treatments

Nursery stock of plum (<u>Prunus salicina</u> Lindel., cv. "Casselman") on Citation (<u>Prunus</u> hybrid) rootstock were planted 1 April 1988 in an experimental orchard at the University of California Kearney Agricultural Center near Fresno, California (lat. 36° 36' N, lon. 119° 30' W). Tree and row spacing was 1.83 and 4.27 m, respectively. Trees were trained to an open-vase shape with other cultural practices being similar to those used for the commercial production of plums. Trees were irrigated with 200 liter $tree^{-1}$ wk^{-1} via low-volume fan jet sprinklers throughout each growing season.

Open-top chamber frames utilized in this study were constructed from extruded aluminum tube-lock welded to 4 cm thinwall tubing. The chamber dimensions were 3x7x3 (WxLxH) m on a 3x7 m rectangular base of 5x30 cm redwood boards. Chamber frames were initially put around the trees on 4 November 1988. Each chamber contained four plum trees. The chamber air delivery system consisted of a blower located at one end of each chamber with four 23 cm diameter plastic tube (Arizona Bag and Plastic Co., Phoenix, AZ) air ducts running from one end of the chamber to the other along the seven meter chamber length. Two of the air ducts ran along the sides of the chamber at a height of 1.5 meters above the chamber floor. Air from these two ducts was directed towards the middle and top of the tree canopy's within the chamber. An additional pair of air ducts was located directly beneath the trees and this air was directed upwards into the lower canopy. Air from all the ducts passed into the chamber atmosphere through 8.5 cm diamond shaped holes cut every 30 cm in the delivery tubes. This air delivery system provided approximately 133 m^3 min^{-1} air to each chamber, enough to change the air volume in the chambers approximately two times per minute. Clear 12 mil PVC (Goss Products Inc., Corona, CA) walls were first put on the chambers 1-8 May 1989 and chamber blowers were turned on at that time. Chamber blowers were operated 24 hours per day during the growing season.

Ozone treatments imposed in this study were charcoal filtered air (CF), ambient air (AA), and ambient air + ozone (AO). Treatments were randomly assigned to a chamber and there were five replications containing one chamber of each treatment as well as an additional no-chamber treatment plot (NC). Ozone concentrations in the treatment plots were monitored using a computer controlled monitoring system described previously (Retzlaff et al., 1991). A Dasibi Model 1003 AH Ozone Analyzer was used to measure ozone. Calibration occurred weekly and involved cleaning and frequency count checks. Also, each Spring and Fall all ozone analyzers were checked for drift against an ozone analyzer provided by the State of California Air Resources Board. Ozone treatments were initiated on 1 and 8 of April 1991 and 1992, respectively, and continued until 31 October, 1991 and 1 November 1992. Trees were exposed to ambient air during the remainder of the year.

Trees from one replication (previous replication three) were enclosed in open-top fumigation chambers and exposed to the three ozone treatments (as described above) from 30 April to 23 August in 1993. The remaining treatment plots (redesignated as the post-chamber [PC] treatment; previous replications 1, 2, 4, and 5) were not enclosed or exposed to different ozone concentrations during the 1993 growing season.

Air for the ambient treatment was blown directly into the chamber. Air for the charcoal filtered chambers was first drawn through activated charcoal filters before delivery into the chambers. Ozone for the ambient + ozone treatment chambers was generated from ambient air with a Griffin (Lodi, NJ) Model GTC-2A Ozone Generator and delivered via Teflon tubing to the delivery air stream of these chambers. The ozone generator was computer automated to increase or decrease the ozone output from 0800 to 2000 h Pacific Daylight Time (PDT) depending on the ambient atmospheric ozone concentration.

Final ozone concentration data analysis was conducted utilizing the means procedure (Proc Means) of the statistical analysis system (SAS Institute, 1985). Ozone 12-h means (0800-2000 h PDT) were calculated for each treatment. These ozone concentrations were used to assess the effects of ozone air pollution on tree growth, development, and yield.

Gas Exchange

Three weeks after treatment initiation, leaf net CO_2 assimilation was measured on all trees in the study plots. This process was repeated at three-week intervals and each tree was measured nine times in 1992. On each measurement day, leaf net CO_2 assimilation was measured on one leaf from each tree in every treatment (20 leaves/treatment, 80 total leaves per sample day). Fully expanded leaves that had been in direct sunlight prior to data collection were selected for measurement. Measurements were made between 1000 and 1200 h and leaf temperatures and photon flux density (PFD) averaged 20°C and 1000 μmol m^{-2} s^{-1}, respectively, across all dates. Following measurement, the leaves were harvested from the tree and their actual leaf surface area determined with a Li-Cor (Lincoln, NE) Model LC3100 Leaf Area Meter.

All photosynthesis measurements were made utilizing an Analytical Development Corporation (Hoddesdon, England) Portable Infrared Gas Analyzer (IRGA) (Model LCA-2), Air Supply Unit with Mass Flowmeter (Model ASUM), Data Processor for the LCA-2 (Model DL-2), and broad leaf Parkinson Leaf Chamber. The IRGA was used in the differential mode and routinely calibrated with a "Primary Standard" of CO_2 (350 ppm) in air (Matheson Gas Products, Secaucus, NJ). Air for the leaf chamber was taken from the open-top chamber in which the tree was growing.

Growth Measurements

Circumference of each tree trunk was measured at monthly intervals from 1 May through 1 December in 1991, 1992, and 1993. Painted bands on the trees eighteen centimeters above the soil-line were used as reference points in order to minimize measurement errors. The increase in trunk cross-sectional area from 1 May to 1 December was calculated from the circumference measurements. Data were analyzed on a per tree basis. Trees also were visually inspected for foliar symptoms of chronic ozone injury when measurements were taken.

Leaf-fall was measured by collecting the leaves on the ground below the trees in the chamber treatments (charcoal filtered, ambient, and ambient + ozone) at various times throughout the growing season. All leaves on the ground below the trees were collected and any remaining foliage on the trees was stripped off in order to determine final foliage biomass at the end of the season. Data were analyzed on a per plot (chamber) basis.

Trees in the present study were dormant pruned on 14, 24, and 28 January 1992, 1993, and 1994, respectively. Fresh prunings were weighed and then placed in a forced air oven at 70°C until there was no further weight change and final dry weight determined. Pruning weights were analyzed on a per tree basis.

Fruit Yield

Differences in fruiting potential among trees in the four treatments was determined by counting all flowers on two trees in each plot just prior to full bloom (16, 11, and 19 February 1991, 1992, 1993, respectively). After fruit set, any fruit that fell from the trees were picked up, counted, and added to total fruit number after harvest. At fruit maturity, fruit from individual trees in each treatment was picked. Harvest dates were 21 August 1991, 5 August 1992 and 5 August 1993.

Statistical Analysis

The main experimental design was a randomized complete block with 3 ozone (CF, AA, and AO) treatments and 5 replications. The experiment was replicated/blocked five times to account for chamber location in the field and possible soil differences among chambers except in 1993. The last year of the study, data were collected on the four individual trees in each treatment of replication three. Data for measurements that were repeated throughout the study were analyzed using a repeated measures analysis of variance with two grouping factors (replication and treatment) and one within factor (time). Data collected on individual dates and/or only once during the study were analyzed by two-way ANOVA. In all analyses, linear contrasts with the 12-hour mean ozone levels were used for *a priori* comparisons among treatment means (α

< 0.05). In addition, two-way ANOVA was used to compare the responses of trees in the ambient chambers with those of the no-chamber plots. Similar analyses were used in 1993 for the PC treatments.

RESULTS

Ozone Treatments

In 1991, seasonal 12-h mean ozone concentrations in CF were 68% of those in AA, whereas those in AO were 188% of those in AA (Figure 2). In 1992, seasonal 12-h mean ozone concentrations in CF were 60% of those in AA, whereas those in AO were 193% of those in AA. In 1993, seasonal 12-h mean ozone concentrations in CF were 77% of those in AA, whereas those in AO were 223% of those in AA. Ozone concentrations in AA were 86, 83, and 85% of those in NC in 1991, 1992, and 1993, respectively. Ozone concentrations in the PC treatments (0.052 ppm, 1993 only) were 95% of those in the NC treatment plots.

Gas Exchange

Leaf net CO_2 assimilation rate of "Casselman" plum was reduced in the AA and AO treatments when compared to the CF treatment four months after treatments were initiated in 1992 (Figure 3). Further reductions in "Casselman" plum leaf net CO_2 assimilation in the AA and AO treatment chambers occurred on the remaining measurement dates. There was no difference in "Casselman" plum leaf net CO_2 assimilation between the AA and NC plots.

Tree Vegetative Growth

Three Year Ozone Study

Trunk cross-sectional area growth of "Casselman" plum was increased by increased atmospheric ozone concentrations in 1992 (Figure 4, Table 1). Trunk cross-sectional area growth of NC trees was less than that of AA trees in 1991, but was the same in 1992 and 1993. Dormant pruning weights across all three exposure years were similar among all treatments (Figure 5, Table 1).

Post-Chamber Study

Trunk cross-sectional area growth of PC trees (1993 only) was the same regardless of the previous ozone treatment (data not given). Pruning weights of PC trees (1993 only) were the same regardless of the previous ozone treatment (data not given).

Foliar Injury

Visual injury, in the form of chlorotic spots and yellow flecking on the leaf surface of older foliage, was observed on "Casselman" plum trees in the AO treatment approximately two months following treatment initiation in each of the three growing seasons. As the growing season progressed, foliar ozone injury increased and some leaf abscission of injured foliage occurred. By 10

November in all three growing seasons, > 85% of the total foliage remained on the CF and AA trees while < 73% of the total foliage remained on the AO trees (Figure 6, Table 1). Following an application of a foliar fertilizer (36% Zinc Sulfate; 16.8 kg ha^{-1}) on 7 November, 6 November, and 26 October (in 1991, 1992, and 1993, respectively) most of the remaining foliage on trees in all the treatments abscised. Final cumulative foliage dry weight was similar across all three years in all the chamber treatments (Figure 7, Table 1).

Fruit Yield

Three Year Ozone Study

Fruit yield per tree and per hectare was reduced in the AA and AO compared to the CF treatment in all three exposure years (Table 2). Differences in yield among ozone treatments were primarily related to differences in total number of fruit per tree rather than average fruit size (Table 2). In one year (1992) average fruit size of the AO treatment was actually greater than the other treatments. There was a linear reduction in yield with an increase in mean ozone concentration each growing season (Figure 8).

The cause of the differences in number of fruit harvested per tree varied among years. In 1991 the mean number of flowers per tree was similar among treatments but the percent fruit set was significantly reduced in the AO treatment trees (Table 3). In 1992, higher ozone treatments had significantly fewer flowers at bloom but percent fruit set and percent fruit drop were unaffected. In 1993, initial flowers numbers appeared lower in the high ozone treatments but the differences were not statistically significant. In that same year, percent fruit set appeared unaffected by ozone treatment but percent fruit drop during the growing season was substantially increased.

The yield of trees outside the chamber (NC) was similar to the trees exposed to ambient ozone within the chambers in 1991 and 1992 but greater in 1993. The yield differences in 1993 were due to greater fruit numbers per tree and not fruit size; the greater fruit numbers per tree were primarily related to decreased fruit drop in the NC trees compared to the AA trees (Table 3).

Post-Chamber Study

Yield and components of yield were the same for all PC treatment plots in 1993 regardless of the preceding years ozone exposure regime (Table 4). Similarities in yield were due primarily to increased fruit abscission in the previous CF treatment.

Simulation Model

The PEACH photosynthesis/carbon allocation simulation model was adapted for plum trees used in this study. The fresh weights of individual plum fruit were successfully predicted by the model to within one standard error of actual weight (Figure 9). The model also predicted final yield of trees in the CF and AO treatments again to within one standard error of the actual yield except for the CF treatment in 1992 (Figure 10). The reason is unknown for that particular discrepancy. The model predicted differences in canopy photosynthesis beginning on April 16, however, the reductions in cumulative assimilation caused by ozone were less than 10% until June 20 each year (Figure 11). At the time of harvest in mid-August, cumulative assimilation was 17% lower in the high ozone (AO) treatment compared to the trees exposed to charcoal filtered air.

DISCUSSION

Leaf net CO_2 assimilation rate of "Casselman" plum was reduced in atmospheres containing ambient and twice ambient ozone concentrations compared to charcoal filtered air in 1992 (Figure 3). Similar results for "Casselman" plum were reported previously (Retzlaff et al., 1991; Retzlaff et al., 1992b). In all three studies, decreases in leaf CO_2 assimilation were not immediately apparent and only developed after an extended exposure period. In the absence of ozone, leaf photosynthetic capacity peaks early in the season and then declines gradually thereafter until leaf abscission (Pye, 1988). This pattern was exhibited by "Casselman" plum growing in charcoal filtered atmospheres and to a certain extent in the ambient ozone atmosphere. Increasing the atmospheric ozone concentration up to two-times the ambient level resulted in a more rapid decline in leaf CO_2 assimilation. Ozone has previously been found to accelerate the seasonal decline in photosynthetic capacity (Reich, 1983).

Trunk cross-sectional area growth of "Casselman" plum was not affected (1991 and 1993) or was increased (1992) by ozone concentrations that were near two-times the ambient level (Figure 4). Previously, trunk cross-sectional area growth of plum in a newly established orchard was found to decrease linearly with increasing ozone concentration (Retzlaff et al., 1991; Retzlaff et al., 1992b). The decrease in plum trunk growth in the previous reports was apparently related to the decrease in photosynthesis and loss of photosynthetic leaf area of these newly established plum trees in response to increased ozone concentrations. As fruit trees progress from the orchard establishment period to commercial bearing-age there is a shift in carbohydrate allocation from vegetative growth to fruit production. One hypothesis for the similarity (1991 and 1993) and increase (1992) in plum trunk cross-sectional area growth in the AO treatment compared to the other treatments in this study could be attributed to additional photosynthate available to the AO trees because of the reduced fruit load on these trees (Figure 8, Table 3).

Other measures of vegetative growth for these plum trees also were unaffected by increased ozone concentrations. Dormant pruning weights (Figure 5) were similar across ozone treatments each growing season further illustrating the lack of a vegetative growth response by "Casselman" plum to changes in atmospheric ozone concentration. Retzlaff et al. (1991 and 1992b) reported that shoot length, leaf number, numbers of lateral branches and dormant pruning weights of newly established "Casselman" plum trees were unaffected by increased ozone concentration. Ozone apparently alters height growth differently than diameter for plum, as has been reported previously for other trees (Pye, 1988). In contrast, beech (Fagus sylvatica L.) exposed to ozone during the previous growing season had a reduced rate of shoot elongation during the first week after bud break and a reduced (17% less) amount of total seasonal growth which was the result of reduced internodal expansion (Pearson and Mansfield, 1994). The ozone response difference among studies could be that the majority of height growth in fruit trees occurs early in the growing season before the ozone treatments affect photosynthesis (Retzlaff et al., 1991, 1992b), whereas, fruit tree diameter growth continues throughout the entire growing season (DeJong et al., 1987).

Foliar injury occurred on "Casselman" plum trees only in the AO plots in the present study and was similar to that reported previously for this plum cultivar and for other tree species (Chappelka et al., 1988; Keane and Manning, 1988; Retzlaff et al., 1991, 1992a, 1992b; Scherzer and McClenahen, 1989). In addition, premature leaf senescence of the injured foliage occurred (Figure 6) during the exposure of these commercial bearing-age plum trees. Foliar ozone symptoms are often followed by leaf fall (Keller, 1988; Lehnherr et al., 1988; Prinz, 1988; Reich and Amundson, 1985; Retzlaff et al., 1992a, 1992b). In the present study, leaf dry weight produced on the commercial bearing-age plum trees was the same (Figure 7) in all chamber treatments at the end of the growing season indicating that ozone-induced foliar injury did not affect leaf formation or development. Similarly, hybrid poplar (Populus x euramericana) shed their ozone-injured foliage while new foliage developed throughout the growing season resulting in the same total leaf number (compared to poplar exposed to ambient air) measured at the end of the growing season (Matyssek et al., 1993).

Yield data indicate that increased ozone concentrations reduced yield of commercial bearing-age "Casselman" plum (Figure 8). Previously, yield data from this study in 1990 (the first bearing year in this orchard) also indicated that increased ozone concentrations decreased "Casselman" plum yield (Retzlaff et al., 1992b). Similarly, yield of 'Valencia' orange(Citrus sinensis [L.] Osbeck) and 'Heritage' raspberry (Rubus idaeus L.) decreased with increasing ozone concentration (Olszyk et al., 1990; Sullivan et al., 1994). The ozone induced yield reduction in "Casselman" plum is due entirely to the reduction in the number of fruit per tree which is different than reported in the 'Valencia' orange study (reduced fruit number and fruit size), but similar to 'Heritage' raspberry (reduced fruit number) (Olszyk et al., 1990; Sullivan et al., 1994). The decrease in yield of 'Heritage' raspberry in the second year of that study was attributed to decreases in berry count which suggested a reduction in yield potential due to fewer flowers; however, flowers were not counted (Sullivan et al., 1994). Flower and fruit drop counts, and percent fruit set responses of "Casselman" plum measured (Table 3) in the present study varied from year to year gave no clear indication of the exact physiological mechanism that causes the measured yield reduction (lower fruit counts) in response to increased ozone concentration. It is clear however, that ozone exposure did not reduce "Casselman" plum fruit size although ozone exposure can reduce "Casselman" plum fruit postharvest quality (Crisosto et al., 1993). In a recent review of carbon allocation in trees, Cannell and Dewar (1994) state that during the period of endosperm filling, the growth rate of seeds tends to be constant, and the final weight per seed is usually much less variable than the number of seeds produced per plant. Further, trees have developed a number of mechanisms to adjust the total number of seed or fruit that are set to ensure that the assimilate and nutrient resources are adequate to produce full-sized seed or fruit without threatening the survival of the vegetative structure. It appears in the present study that "Casselman" plum has adopted this partitioning strategy of adjusting the total number of fruit per tree in order to alleviate the stress associated with less carbon assimilation (Retzlaff et al., 1991, 1992b) to increased ozone concentrations.

Growth and yield of commercial bearing-age "Casselman" plum trees grown outside the chamber (NC) in ambient concentrations of ozone was approximately the same as those of trees grown in the AA chambers even though the ozone concentration was reduced by as much as 17% in AA compared to NC. In addition, yield of PC trees (previously exposed to various ozone concentrations) in 1993 was similar to that of AA and NC trees. In a study of the effects of ambient air pollution in open-top chambers on bean (Phaseolus vulgaris L.) it was noted that the presence of the chamber had opposite effects on yield in successive years (Schenone et al., 1992). In one growing season the no-chamber bean yield was 30% less than that in the chamber, while in the next growing season bean yields in the chamber were 70% less than that in the no-chamber plots. The results indicate that chamber effects on bean yield may be related to different seasonal and plant maturity conditions. As reported previously (Retzlaff et al., 1992b) and in the present study, the open-top chambers apparently had little effect on the overall physiology and yield of "Casselman" plum trees over multiple growing seasons.

Yields of "Casselman" plum trees in the PC treatment were the same regardless of the previous four seasons ozone exposure (Table 4). The similarity in yield of the PC trees previously exposed to CF compared with the previous AA treatment indicate that a decrease in air quality (increased seasonal ozone concentration) can apparently reduce yield of "Casselman" plum trees. Conversely, the similarity in yield of the PC trees previously exposed to AO compared with the previous AA treatment indicates that an improvement in air quality (decreased seasonal ozone concentration) can increase yield of "Casselman" plum trees. These results also indicate that the previous years ozone exposure level does not completely determine the yield of "Casselman" plum the following year, an important implication further indicating that a combination of factors determine the yield response of fruit tree crops to ozone air pollution.

The adapted PEACH simulation model successfully predicted fruit size and final yields of trees exposed to the two extreme ozone treatments used in this study. At no time during the course of this study was fruit size reduced to increased seasonal ozone exposure. Because exposure to greater concentrations of ozone reduces fruit number, the carbon demand for fruit growth is lower for ozone-exposed trees. In the simulations, the reductions in carbon assimilation caused by increased ozone were less than the reductions in carbon demand for fruit growth. For this reason fruit size was not reduced by ozone.

The model successfully predicted final yield owing in part to the fact that fruit number is input into the model. The model does not make predictions about flower bud development for the subsequent year. Our understanding of the internal and external factors determining flower bud differentiation, fruit set and fruit abscission in trees is insufficient to conclude that reduced amounts of carbohydrates, as demonstrated in Figure 11, were responsible for the observed effects of greater concentrations of ozone on reductions in fruit number and subsequently final yield.

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Table 1. Probabilities of statistically significant ozone treatment effects for trunk cross-sectional area growth (Figure 4), dormant pruning weights (Figure 5), leaf weight remaining on the tree (Figure 6), and total leaf dry weight (Figure 7) of "Casselman" plum exposed to different seasonal ozone concentrations in 1991, 1992, and 1993.

	Trunk cross-sectional area growth	Dormant pruning weight	Leaf weight remaining on tree	Total leaf dry weight
		1991		
Linear	NS	NS	*	NS
AA vs. NC	*	*	-	-
		1992		
Linear	*	NS	*	NS
AA vs. NC	NS	NS	-	-
		1993		
Linear	NS	NS	*	NS
AA vs. NC	NS	NS	-	-

A significant linear treatment effect (*) indicates that each mean from the CF, AA, and AO treatments is different at the 5% level.

A significant treatment effect (*) indicates that each mean from the AA and NC treatments is different at the 5% level.

Foliage was not collected on the ground below the NC trees, so no comparison with the AA treatment could be made.

Table 2. Total number of fruit at harvest, average fruit weight, fruit weight per tree, and fruit weight per hectare of "Casselman" plum trees exposed to different atmospheric ozone partial pressures in 1991, 1992, and 1993.

Ozone Treatment	Total # of fruit/tree at harvest	Average fruit weight (g)	Yield (kg/tree)	Yield (kg/ha)
		1991		
CF	227 (16)	87 (1.7)	19.8 (1.5)	25291 (1992)
AA	191 (14)	84 (1.7)	15.9 (1.3)	20390 (1609)
AO	79 (11)	82 (2.4)	6.8 (1.0)	8715 (1259)
P>F	*	NS	*	*
NC	212 (23)	75 (1.3)	15.8 (1.7)	20160 (2157)
P>F	NS	*	NS	NS
		1992		
CF	348 (29)	80 (2.1)	27.4 (2.1)	35008 (2684)
AA	306 (26)	80 (2.4)	23.7 (1.7)	30290 (2213)
AO	242 (26)	86 (1.7)	20.5 (2.1)	26241 (2737)
P>F	*	*	*	*
NC	262 (22)	78 (1.8)	19.9 (1.5)	25490 (1935)
P>F	NS	NS	NS	NS
		1993		
CF	217 (4)	88 (2.7)	19.1 (0.8)	24409 (1001)
AA	166 (13)	88 (1.7)	14.5 (1.3)	18598 (1638)
AO	103 (44)	84 (2.2)	8.8 (3.9)	11309 (5017)
P>F	*	NS	*	*
NC	243 (17)	83 (0.3)	20.1 (1.4)	25760 (1841)
P>F	*	*	*	*

n=20 for total # of fruit and yield per tree.

Numbers in parenthesis represent ± one standard error.

Other information as found in Table 1.

Table 3. Total flower number, total fruit set, percentage set, fruit number abscised, and percentage drop of "Casselman" plum trees exposed to different atmospheric ozone partial pressures in 1991, 1992, and 1993.

Ozone Treatment	Total # flowers per tree	Total # fruit set/tree	% Set	Fruit abscised per tree	% drop
			1991		
CF	6817 (594)	363 (48)	5.3 (0.3)	137 (25)	37 (2.4)
AA	6913 (741)	296 (32)	4.3 (0.2)	105 (13)	35 (0.7)
AO	5468 (500)	126 (20)	2.2 (0.2)	47 (7)	35 (2.4)
P>F	NS	*	*	*	NS
NC	6113 (388)	288 (31)	4.9 (0.7)	77 (9)	27 (0.3)
P>F	NS	NS	NS	NS	NS
			1992		
CF	9162 (739)	622 (90)	6.7 (0.7)	274 (58)	42 (4.4)
AA	6989 (892)	495 (74)	7.1 (0.7)	189 (30)	38 (1.0)
AO	5319 (777)	395 (61)	7.5 (0.4)	153 (23)	39 (2.5)
P>F	*	NS	NS	NS	NS
NC	6694 (773)	395 (46)	5.9 (0.5)	133 (13)	34 (2.0)
P>F	NS	NS	NS	NS	*
			1993		
CF	9407 (345)	432 (4)	4.6 (0.1)	214	50 (0.4)
AA	7249 (1116)	332 (13)	4.6 (0.2)	167	50 (1.8)
AO	5930 (128)	342 (44)	5.8 (0.7)	239	73 (8.0)
P>F	NS	NS	NS	-	*
NC	9748 (1142)	366 (17)	3.8 (0.2)	123	34 (1.7)
P>F	NS	NS	*	-	*

Total number fruit set per tree = fruit number at harvest (Table 2) + fruit abscised per tree.

Percentage set = (total number fruit set per tree/total number flowers per tree)*100.

Percentage drop = (fruit abscised per tree/total number fruit set per tree)*100.

Other information as found in Tables 1 and 2

Table 4. Total flower number, total fruit set, percentage set, fruit number abscised, percentage drop, total number of fruit at harvest, average fruit weight, fruit weight per tree, and fruit weight per hectare of "Casselman" plum trees exposed to different seasonal ozone concentrations from 1989 through 1992, but not exposed in 1993 (ie. PC Treatments).

1991-1992 Ozone Treatments	Total # flowers per tree	Total # fruit set/tree	% Set	Fruit abscised per tree	% drop
CF	9062 (639)	432 (36)	4.9 (0.6)	240 (16)	56 (4.5)
AA	8481 (404)	383 (33)	4.5 (0.2)	164 (12)	43 (0.9)
AO	7991 (765)	324 (40)	4.3 (0.8)	127 (14)	39 (1.2)
P>F	NS	NS	NS	*	*
NC	9623 (820)	416 (46)	4.3 (0.4)	157 (30)	37 (3.4)
P>F	NS	NS	NS	NS	NS

	Total # of fruit/tree at harvest	Average fruit weight (g)	Yield (kg/tree)	Yield (kg/ha)
CF	192 (17)	87 (1.8)	16.7 (1.5)	21332 (1949)
AA	219 (17)	82 (1.5)	17.9 (1.3)	22907 (1718)
AO	198 (19)	82 (1.2)	16.0 (1.5)	20505 (1900)
P>F	NS	NS	NS	NS
NC	258 (21)	80 (1.3)	20.4 (1.5)	26084 (1982)
P>F	NS	NS	NS	NS

n = 16 for fruit number at harvest and yield (kg/tree)

Other information as found in Tables 1, 2 and 3.

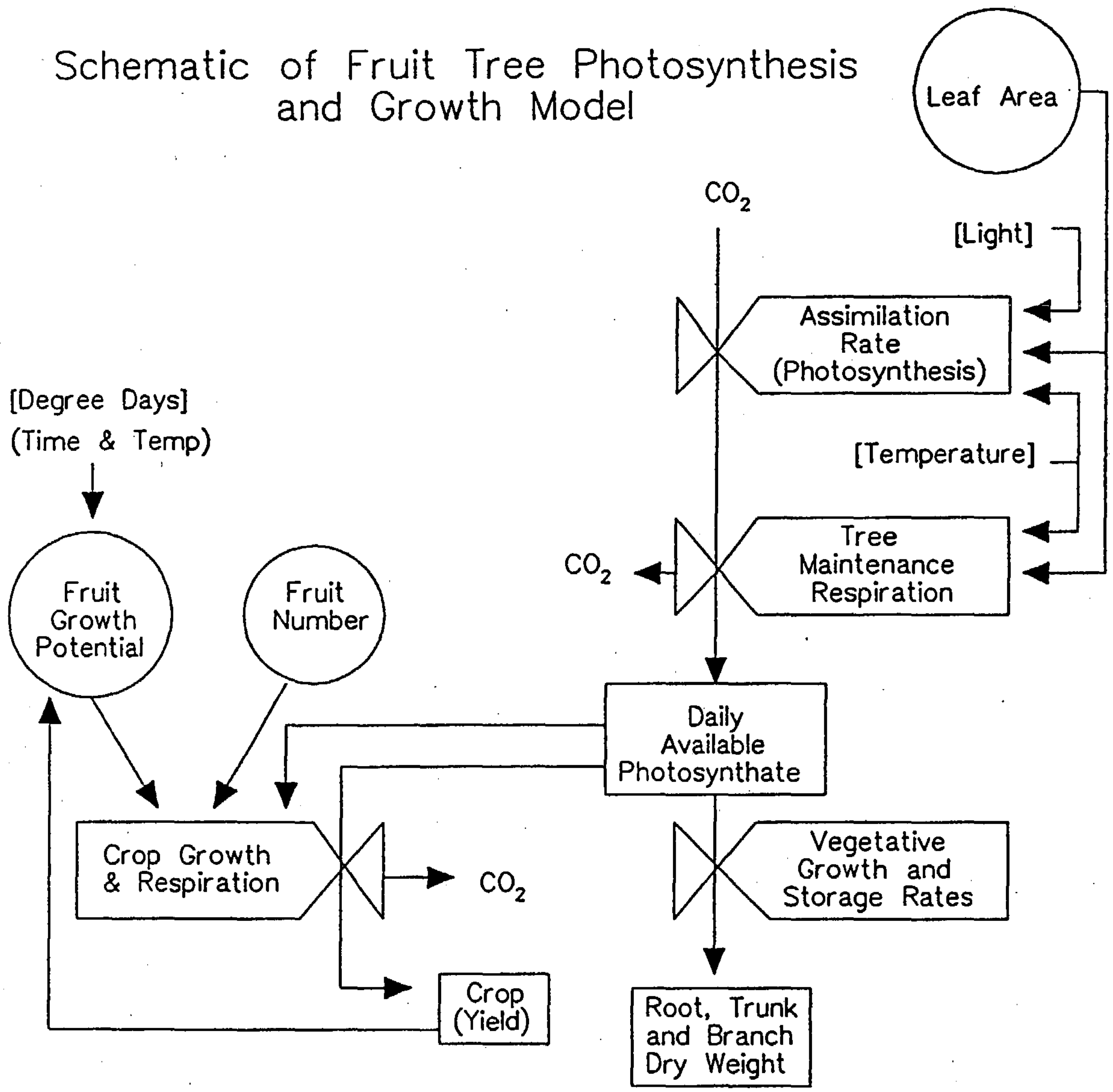

Figure 1. A schematic diagram of the PEACH simulation model. See Grossman and DeJong (1994 b) for further details.

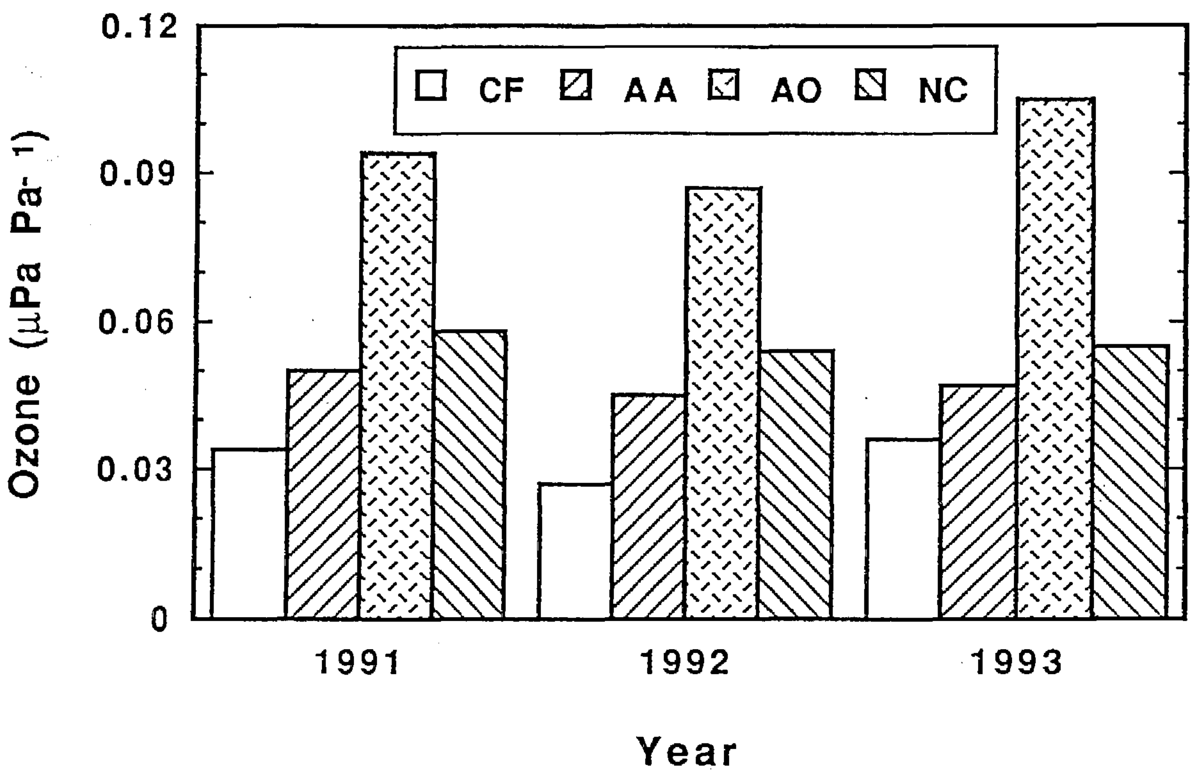

Figure 2. Treatment 12-hour (0800-2000 PDT) mean ozone concentrations for the experimental periods in 1991, 1992, and 1993. The partial pressures of ozone on the y axis are equivalent to ppm.

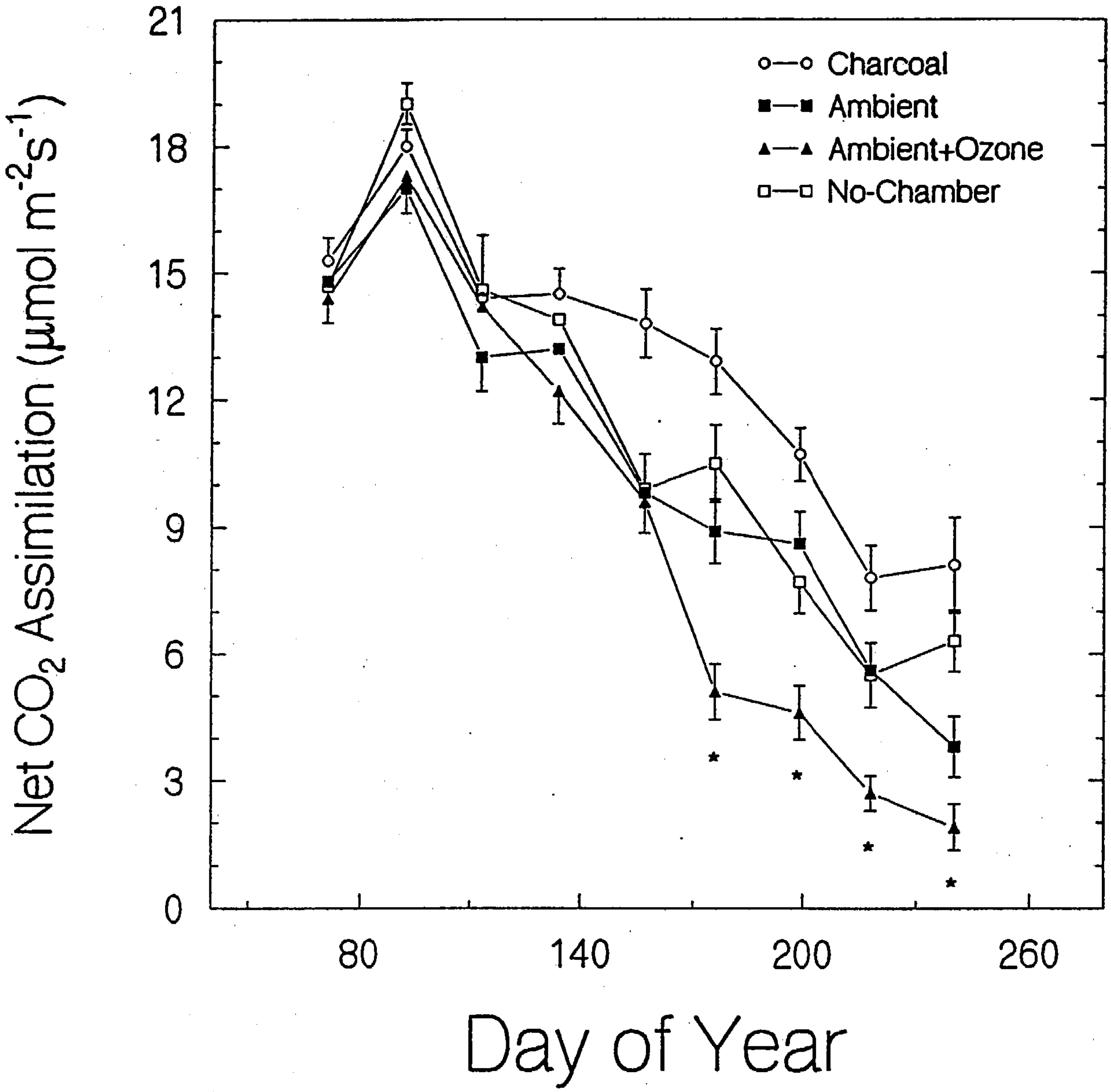

Figure 3. Leaf net CO_2 assimilation (measured at three week intervals) of "Casselman" plum trees exposed to different seasonal ozone concentrations in 1992. Vertical bars represent ± one standard error. Asterisks (*) represent dates on which there was a significant linear treatment effect ($\alpha < 0.05$). n = 20.

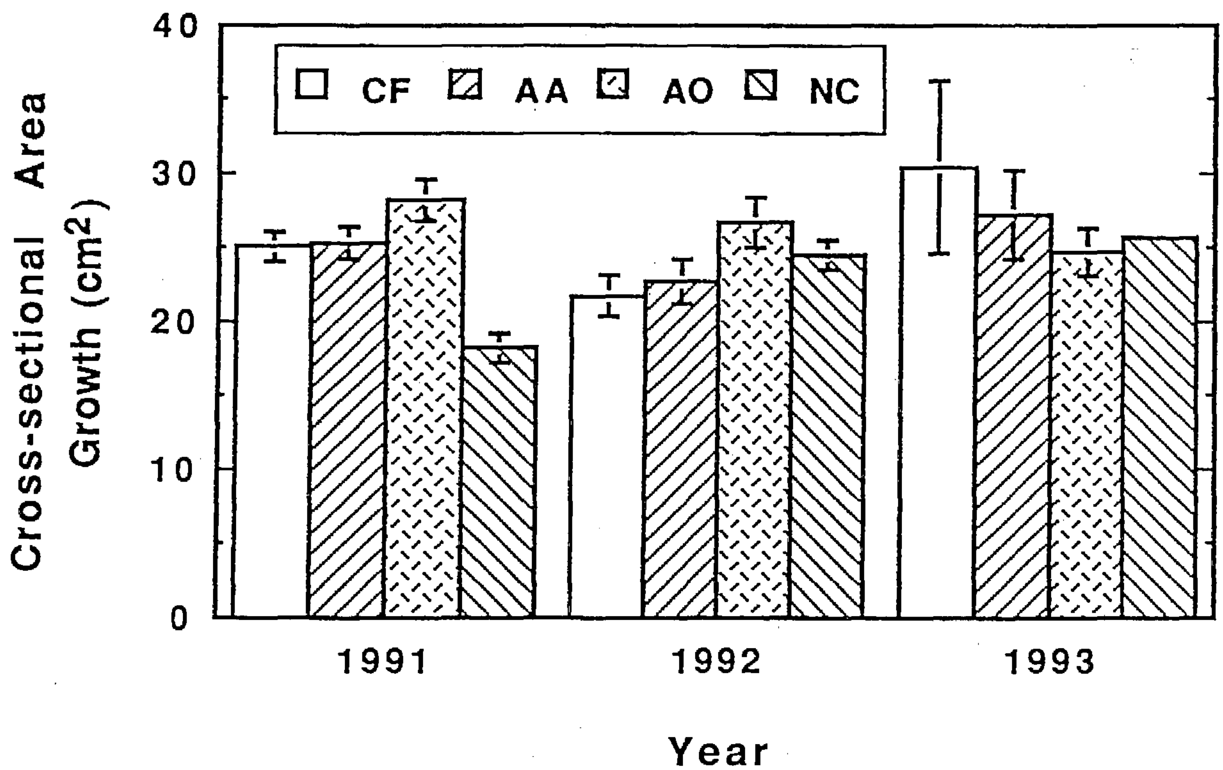

Figure 4. Trunk cross-sectional area growth, during the exposure period, of "Casselman" plum trees exposed to different seasonal ozone concentrations in 1991, 1992, and 1993. Vertical bars represent ± one standard error and are shown when they are larger than the data symbol. There was a significant linear treatment effect only in 1992 (also see Table 1). n = 20 individual trees in 1991 and 1992; n = 4 individual trees in 1993.

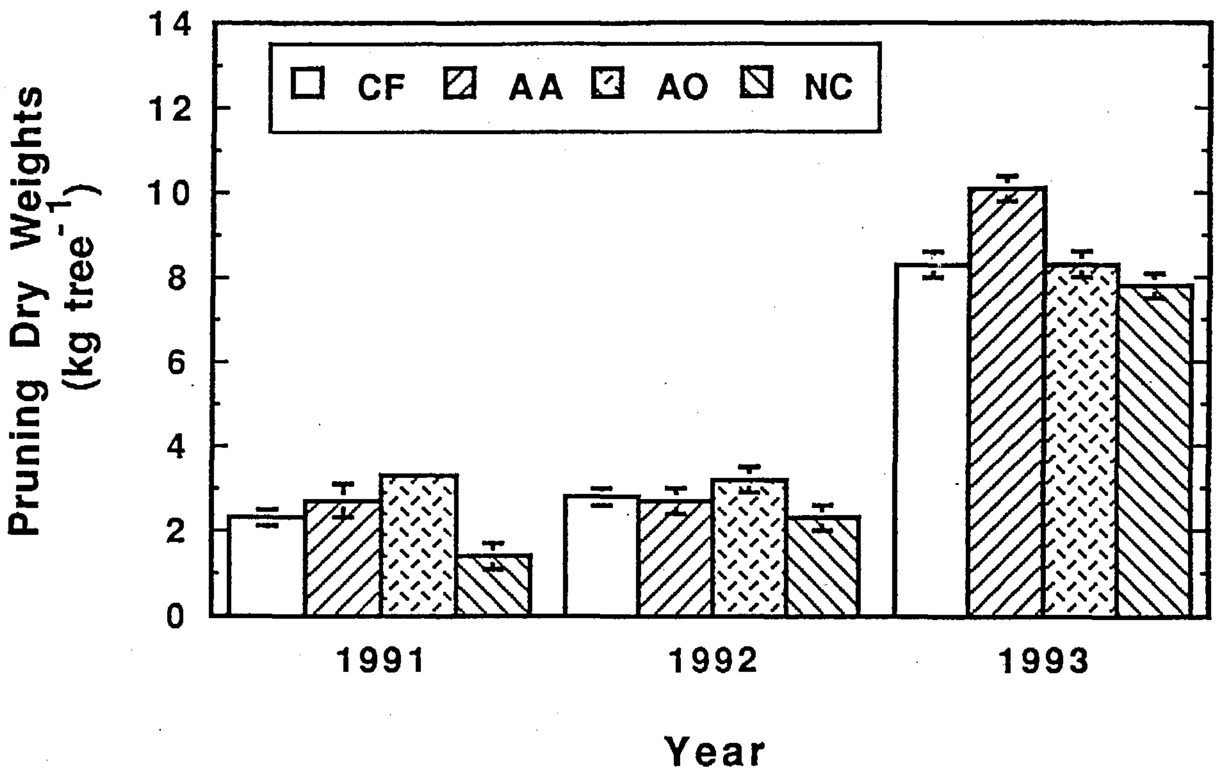

Figure 5. Dormant pruning weights of "Casselman" plum trees exposed to different ozone concentrations in 1991, 1992, and 1993. There were no significant differences found among treatments. n = 20 individual trees in 1991 and 1992; n = 4 individual trees in 1993.

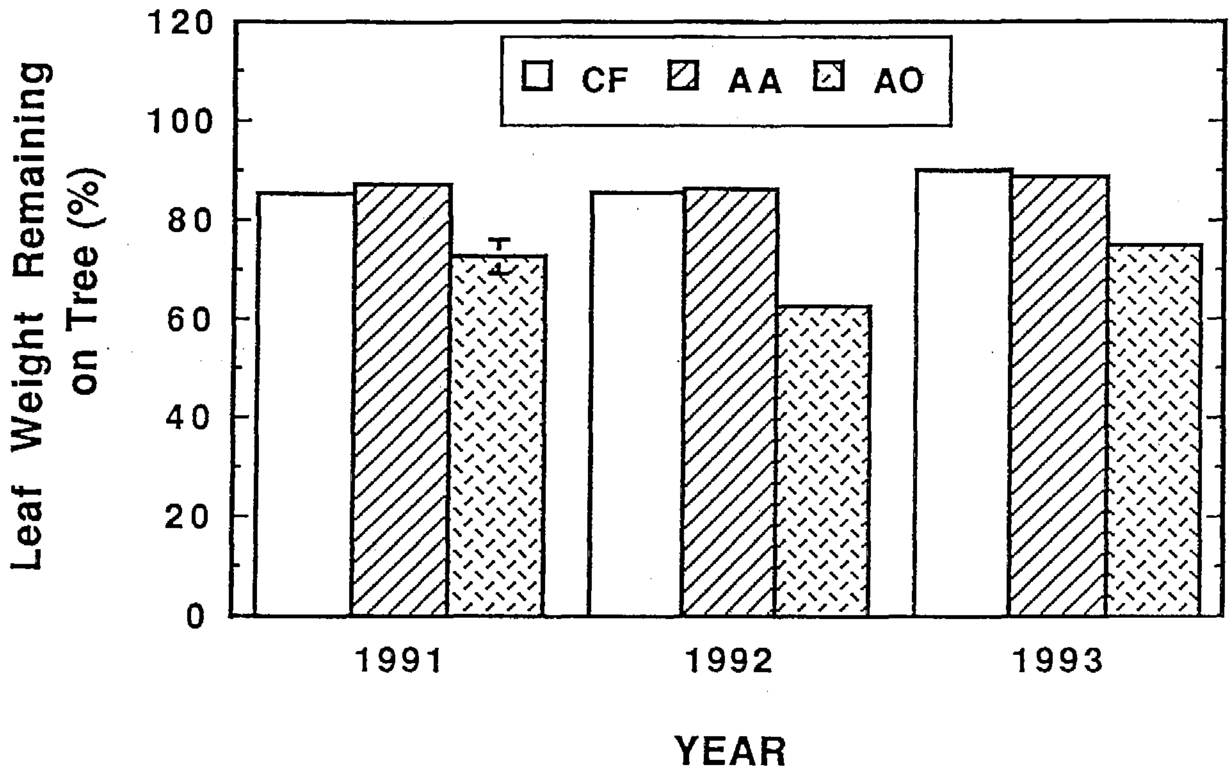

Figure 6. Percentage of total leaf dry weight remaining at the end of growing season on "Casselman" plum trees exposed to different ozone concentrations in 1991, 1992, and 1993. There were significant linear treatment effects each year of the study. Other information as found in Figure 3. Data were collected on a chamber basis; n = 5 in 1991 and 1992; n = 1 in 1993.

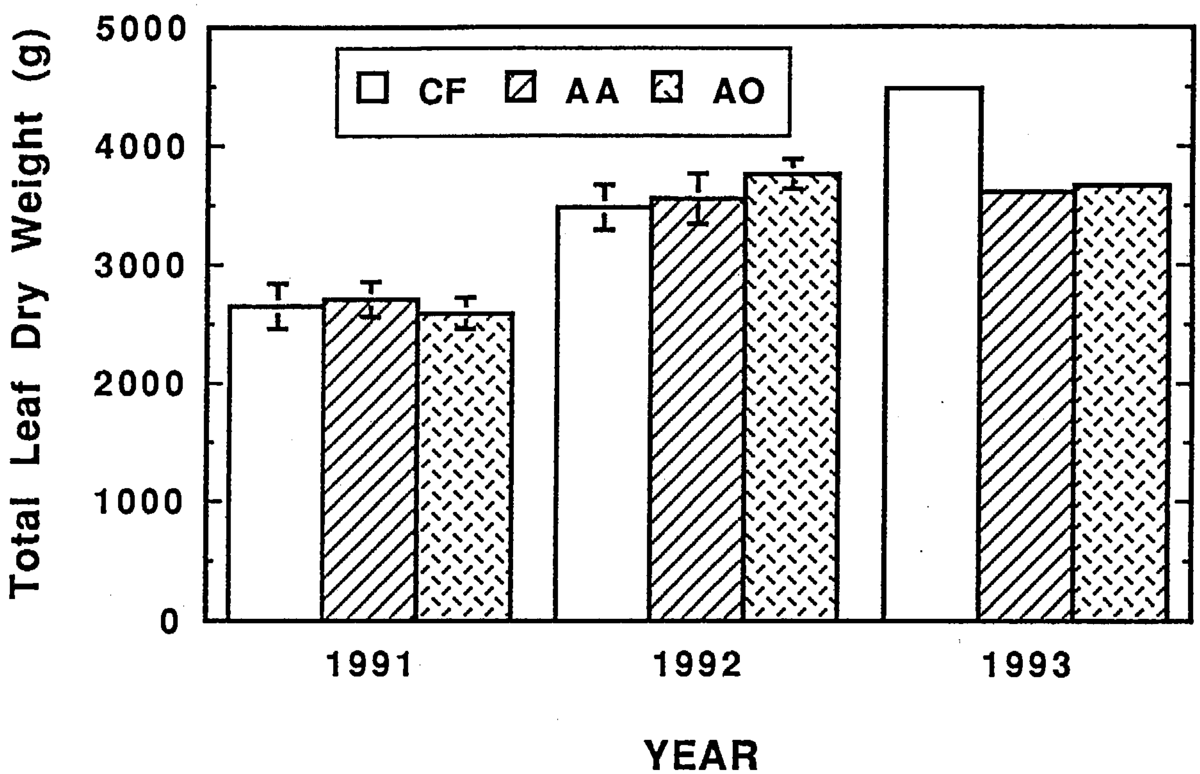

Figure 7. Total leaf dry weight of "Casselman" plum trees exposed to different ozone concentrations in 1991, 1992, and 1993. There were no significant differences among treatments. Other information as found in Figure 3. Data were collected on a chamber basis; n = 5 in 1991 and 1992; n = 1 in 1993.

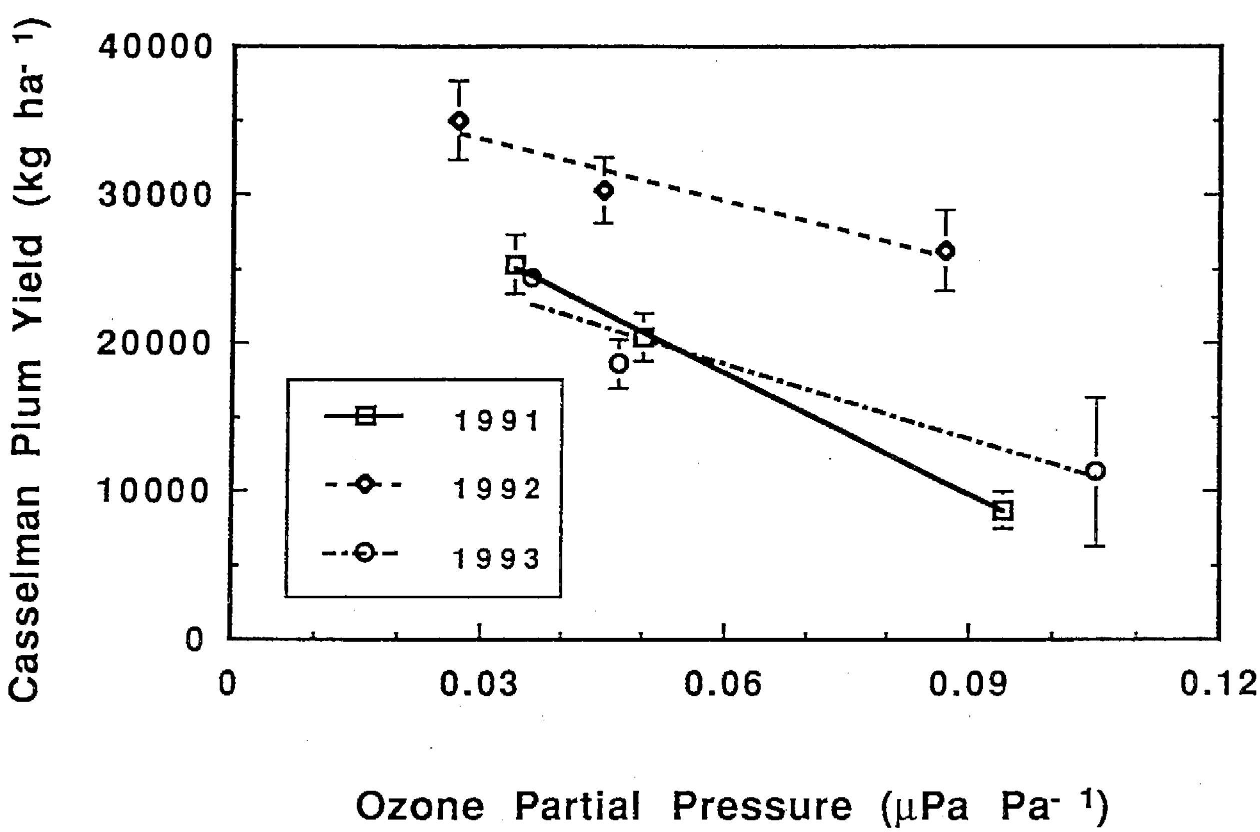

Figure 8. Yield of "Casselman" plum trees exposed to different ozone concentrations in 1991, 1992, and 1993. Other information as found in Figure 3. Yield (1991) = $-273943(O_3) + 34386$, $r^2=0.99$; Yield (1992) = $-137307(O_3) + 37790$, $r^2=0.93$; Yield (1993) = $-168637(O_3) + 3 + 28673$, $r^2=0.91$. Each data point is the mean of 20 individual trees in 1991 and 1992 and four individual trees in 1993. Values of ozone partial pressure are equivalent to ppm.

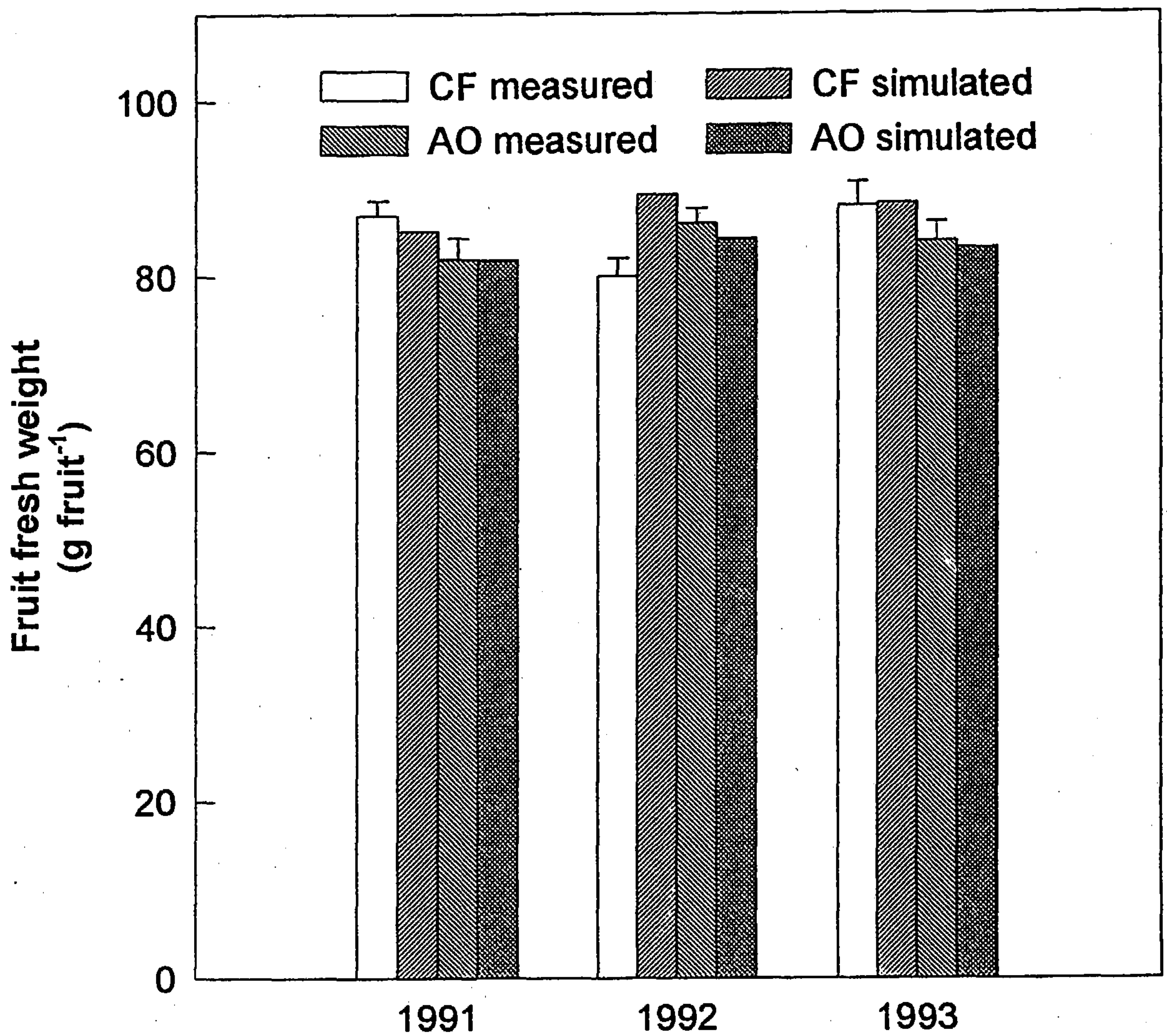

Figure 9. Measured and simulated fruit weights of "Casselman" plums in the two extreme ozone treatments (CF and AO for 1991, 1992, and 1993. Simulated fruit weights were calculated from the PEACH simulation model adapted for plum trees. Bars for measured fruit represent ± one SE.

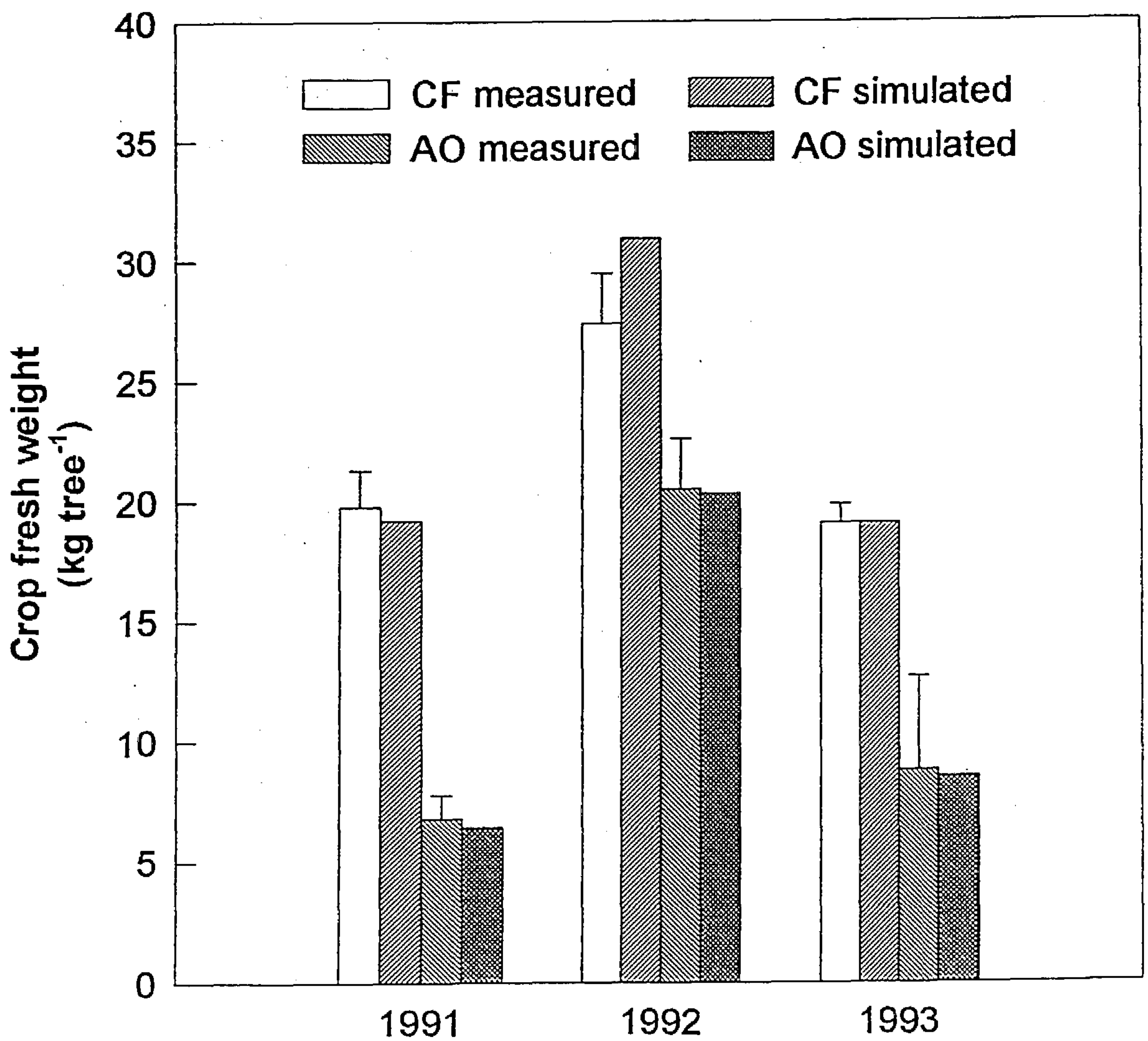

Figure 10. Measured and simulated final yields of "Casselman" plum trees of the AO and CF ozone treatments for 1991, 1992, and 1993. Other information as found in Figure 9.

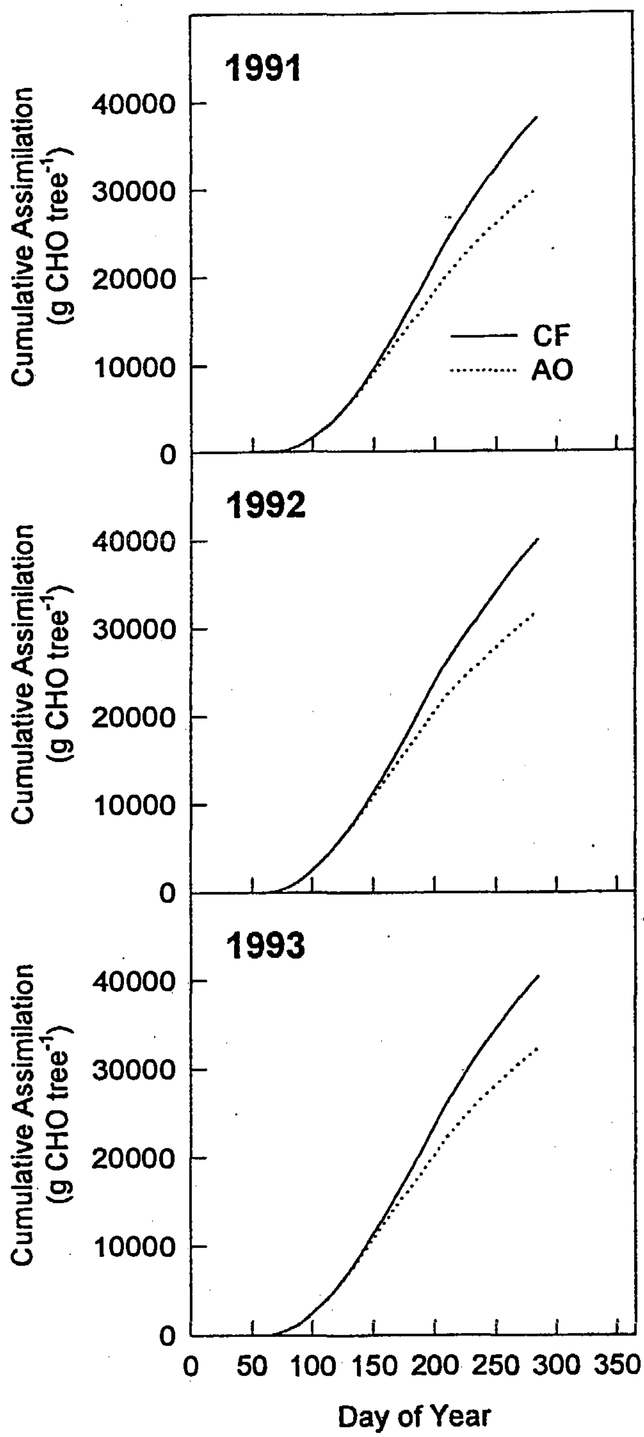

Figure 11. Cumulative carbohydrate (CHO) assimilated by individual "Casselman" plum trees in the CF and AO ozone treatments in 1991, 1992, and 1993. Values were obtained from the simulation model and individual leaf photosynthesis (Figure 3).