

Effects of Low Concentrations of O₃ on Net Photosynthesis, Dark Respiration, and Chlorophyll Contents in Aging Hybrid Poplar Leaves¹

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ABSTRACT

Chronic exposure of hybrid poplar (*Populus deltoides* × *trichocarpa*) plants to low concentrations of ozone had negative impact upon net photosynthetic capacity, dark respiration, and leaf chlorophyll contents. Exposure to as much as 0.20 microliters per liter O₃ had no immediate effect on net photosynthesis (P_n), but chronic exposure to 0.125 or 0.085 microliters per liter had a number of gradual effects on CO₂ exchange. These included increased dark respiration and consequently increased light compensation points in very young leaves (4–6 days old); and decreased P_n , leaf chlorophyll *a* and *b* contents, light saturation points, and apparent quantum yields in leaves 10 to 70 days old. Decreased P_n was partially due to accelerated aging in leaves exposed to O₃, and light-saturated P_n was linearly related to chlorophyll *a* + *b* contents. Differences in light-saturated P_n between control and O₃-treated leaves of the same age were mostly due to photosaturation in O₃-treated leaves and to a much lesser extent to lowered apparent quantum yields. Also, since P_n and dark respiration were most affected by O₃ at different leaf ages, distinct modes of action are suggested. The effects of leaf aging on CO₂ exchange were considerable, but typical of other species. However, careful monitoring of the interacting effects of leaf age and pollutant exposure was needed in order to characterize the impact of chronic O₃ exposure upon CO₂ exchange.

Ozone is currently the most ubiquitous and damaging gaseous air pollutant in industrialized regions of the world. Ozone is phytotoxic at high concentrations (>0.20 $\mu\text{l l}^{-1}$), but until recently little was known about the effects of the lower concentrations (<0.15 $\mu\text{l l}^{-1}$) which are much more typical of concentrations in ambient air, even in most urban locales. Recent studies have found significant negative impact upon growth and yield of a number of species following chronic, low level O₃ exposure (3, 4, 7, 16, 17). Unfortunately, the mechanisms underlying such effects are not well understood. Although exposure to high concentrations of O₃ can have dramatic and rapid effects, such as visible leaf injury, reduced photosynthetic rates, and cell death, extrapolation from such results to the situation at lower concentrations is unrealistic, inasmuch as the sequence of events which

ensues in the latter case is probably different than in the former. Exposure to low concentrations of O₃ will usually not mark leaves or cause cell death, and very little is known about processes such as photosynthesis, respiration, or stomatal function under such circumstances. For these reasons, I examined certain aspects of the net CO₂ exchange of a hybrid poplar (*Populus deltoides* × *trichocarpa*) chronically exposed to approximately 0.08 or 0.12 $\mu\text{l l}^{-1}$ ozone. This paper presents data showing the effects of such exposures upon photosynthetic capacity, dark respiration, and Chl contents in hybrid poplar.

MATERIALS AND METHODS

One hundred and ten cuttings (25 cm in length) of hybrid poplar (Northeastern Forest Experiment Station Clone 207; *Populus deltoides* × *trichocarpa*) were planted in a greenhouse in Ithaca, NY, on April 17, 1981. These cuttings were taken from young trees grown by the author in the field in Ithaca. Cuttings were grown in 19-L pots, in a 1:1:1 mixture (v/v) of peat, vermiculite, and soil, and were fertilized weekly with a 20:20:20 NPK mixture (Peters General Purpose 20-20-20; Peters Fertilizer Products, Fogelsville, PA). On May 5, 10 plants to be used for CO₂ exchange measurements were placed in each of four controlled environment growth chambers (Western Environmental, Napa, CA). Air in the growth chambers was drawn from outdoors through Purofil filters (Purofil Corporation, Chamblee, GA) which removed most of the ambient O₃. Chamber conditions included 16-h photoperiods with half light intensity for the first and last half hours of each photoperiod. Day/night temperatures and relative humidities were 25/20 ± 1°C and 60/70 ± 5%, respectively. PAR at the top of the plant canopy was about 900 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and was measured with a quantum sensor (LI-COR LI-190s).

Four approximate pollutant treatments were chosen (filtered air/control, 0.04, 0.08, and 0.12 $\mu\text{l l}^{-1}$ ozone) and were assigned randomly to the four growth chambers. Ozone was generated by passing O₂ by a UV light source and bled into the chambers. Air in the chambers was sampled using Teflon lines, and concentrations of O₃ were measured by a chemiluminescent monitor (Monitor Labs model 8410E) and continuously recorded (Leeds and Northrup Speedomax M). A switching system was used to alternately monitor air quality in each chamber, for 15 min at a time, except during intensive measurements of CO₂ exchange. At such times, air quality in each chamber was monitored for approximately 5 min of each 20-min period, and line switching was done manually.

Plants were exposed to O₃ for approximately 5.5 h d⁻¹ on 62 d during the 67-d experimental period. Total treatment mean concentrations during all exposures were 0.025 (filtered air),

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0.050, 0.085, and 0.125 $\mu\text{l l}^{-1}$ ozone, respectively. Daily mean concentrations during exposures were always within $\pm 0.01 \mu\text{l l}^{-1}$ of the respective treatment mean concentrations.

Net photosynthetic rates (P_n ³) were assessed in the growth chambers for intact, individual leaves enclosed in either of two thermoelectrically cooled and heated cuvettes (Portable Environments Cuvette and Temperature Control System, Kananaskis Centre for Environmental Research, Alberta, Canada). Growth chamber air was passed through the cuvette, the air flow rate was continuously monitored, and the difference in the CO_2 concentrations between the air stream entering and leaving the cuvette was continuously measured by an IR CO_2 analyzer (ANARAD model AR-600), and recorded. The cuvette atmosphere was mixed constantly by a fan and tests of either CO_2 or O_3 concentrations found no gradients within the cuvette. The CO_2 analyzer was calibrated daily in the differential mode using certified CO_2 standard gases (Scott Specialty Gases, Plumsteadville, PA). During measurements of CO_2 exchange, air temperature in the cuvette was 25°C and CO_2 concentration ranged between 330 and 340 $\mu\text{l l}^{-1}$. The inner surfaces of the cuvettes were lined with Teflon, but significant absorption of O_3 still occurred. Thus, it was necessary to add additional O_3 to the cuvette in order to match the O_3 concentration in the growth chamber. This was done during all measurements of CO_2 exchange, and O_3 concentrations in the cuvettes were monitored as described above. Areas (one side) of paper replicas of sampled leaves were measured using a leaf area meter (LI-COR model LI-3000), and CO_2 exchange rates were calculated on a one-sided leaf area basis.

Inasmuch as the objectives of this study included characterizing the interacting effects of leaf age and O_3 exposure on CO_2 exchange, measurements of P_n and dark respiration were made on leaves of various ages in all treatments. Leaf ages were monitored by recording the emergence date and node position of each newly emerged leaf throughout the study. Net photosynthetic rates followed a similar daily pattern regardless of age or treatment: they increased rapidly following the beginning of the photoperiod and declined very gradually from midafternoon until the end of the photoperiod.

Measurements of CO_2 exchange were made and recorded at approximately midday for two leaves per day by switching from one cuvette to the other in approximately 10- to 15-min cycles. For many leaves, light response curves were generated (between 1130 and 1530 h EST) by monitoring CO_2 exchange following eight or nine decreasing, and then ascending, step changes in PAR incident upon the adaxial leaf surface. Each light level was maintained until P_n had shifted and equilibrated to the new level. Apparent quantum yields were estimated from the initial slopes of the light response curves.

Because of time and equipment constraints (e.g. four treatments and two cuvettes), CO_2 exchange in plants exposed to 0.050 $\mu\text{l l}^{-1}$ O_3 was infrequently measured. Thus, all the following results and discussion pertain only to the other three treatments.

At the conclusion of the experiment, a 0.78 cm^2 leaf disc was taken from each side of the midvein in the midleaf area in six leaves (different plants) of five ages (three ages in the 0.085 $\mu\text{l l}^{-1}$ treatment) within each treatment. The two discs per leaf were combined into a composite sample and each leaf was considered a replicate sample. Leaf discs were homogenized in 80% acetone and leaf Chl *a* + *b* contents were determined for each sample according to the methods of Arnon (1).

RESULTS

Net Photosynthesis. Exposure to O_3 at concentrations less than 0.20 $\mu\text{l l}^{-1}$ had no immediate or short term (less than 1 d) effect on P_n (data not shown). No changes in P_n were found

following step changes in O_3 concentration between 0.01 and 0.20 $\mu\text{l l}^{-1}$, regardless of leaf age, previous treatment, direction of step change, or duration of O_3 exposure (up to several hours). However, gradual changes in net photosynthetic capacity and in dark respiratory rates were observed to be influenced both by leaf age and chronic O_3 exposure (Fig. 1). Changes in light-saturated P_n associated with increasing leaf age (a rapid rise followed by a gradual decline) were similar to those reported for other species (2, 8, 10). Light-saturated P_n increased rapidly until leaves were about 7 d old, reached a peak at about 11 to 16 d, and then gradually declined with increasing age (Fig. 1A). During the first 7 d, P_n of leaves chronically exposed to 0.125 $\mu\text{l l}^{-1}$ O_3 differed only slightly from control leaves. However, once leaves became fully expanded (after 14 d), P_n in leaves exposed to either 0.085 or 0.125 $\mu\text{l l}^{-1}$ O_3 was always much lower than in similarly aged control leaves. The general aging pattern was evident in all treatments, but exposure to increasing concentrations of O_3 tended to accelerate the rate at which the leaf passed through its photosynthetic, and actual, life cycle (O_3 -treated leaves lived approximately 10 d less than control leaves). Also, P_n increased throughout leaf expansion in control leaves and reached a maximum of 35.7 $\text{mg dm}^{-2} \text{h}^{-1}$ at approximately 16 d, whereas 0.125 $\mu\text{l l}^{-1}$ O_3 -treated leaves reach a maximum P_n of 30.6 $\text{mg dm}^{-2} \text{h}^{-1}$ at 11 d, prior to full expansion.

Dark Respiration. Age-related changes in R_D were also similar to those previously reported for other species (2). Dark respiration increased rapidly until leaves were about 6 d old (to approximately 7 $\text{mg dm}^{-2} \text{h}^{-1}$ in leaves exposed to 0.125 $\mu\text{l l}^{-1}$ O_3), and then rapidly declined to relatively low levels in another 10 d (Fig. 1B). For leaves 4 to 35 d old, R_D in 0.125 $\mu\text{l l}^{-1}$ O_3 -treated leaves was considerably higher than in leaves receiving filtered air. After 35 d, R_D in leaves in the 0.125 $\mu\text{l l}^{-1}$ O_3 treatment was still higher than in similarly aged leaves exposed to filtered air, but differences were small and rates in general were low.

Light Saturation, Light Compensation, and Apparent Quantum Yield. As leaves expanded both the light saturation point and the apparent quantum yield increased in leaves from all treatments (Fig. 2). Differences in light saturation point between control (0.025 $\mu\text{l l}^{-1}$) and high O_3 (0.125 $\mu\text{l l}^{-1}$) treated leaves did not appear until leaves were greater than 10 d old, whereas between-treatment differences in apparent quantum yield were apparent at 5 d of age (Fig. 2, A and C). In contrast, both the light compensation points and the differences in light compensation points between treatments were at their maxima in very young leaves (4 to 5 d old), and declined with increasing age (Fig. 2B). The effect of age on light compensation can be explained by the high dark respiratory rates (Fig. 1B) and relatively low quantum yields of very young leaves. Large differences in light compensation between young control and high O_3 -treated leaves were due to relatively greater dark respiration and lower apparent quantum yields of leaves in the high O_3 treatment.

Once leaves were fully expanded (after 14 d), further changes in light compensation points were minimal, while apparent quantum yields and light saturation points exhibited gradual declines with increasing age (Fig. 2). Differences in apparent quantum yields between leaves exposed to filtered-air and O_3 treatments were relatively stable over that period, while the difference in light saturation of leaves in the various treatments grew continuously larger.

Light Response Curves. The response of P_n to changes in PAR incident upon the adaxial leaf surface (Fig. 3) is determined by quantum yield at lower, nonsaturating light levels, and by gradual photosaturation at increasingly higher light levels, while the y -intercept is a function of dark respiration. The photosynthetic light response of leaves exposed to 0.025, 0.085, or 0.125 $\mu\text{l l}^{-1}$ O_3 for 6, 24, 38, or 58 d was due both to treatment and to leaf age, and was related to the above mentioned photobiological

³ Abbreviations: P_n , net photosynthesis; R_D , dark respiration.

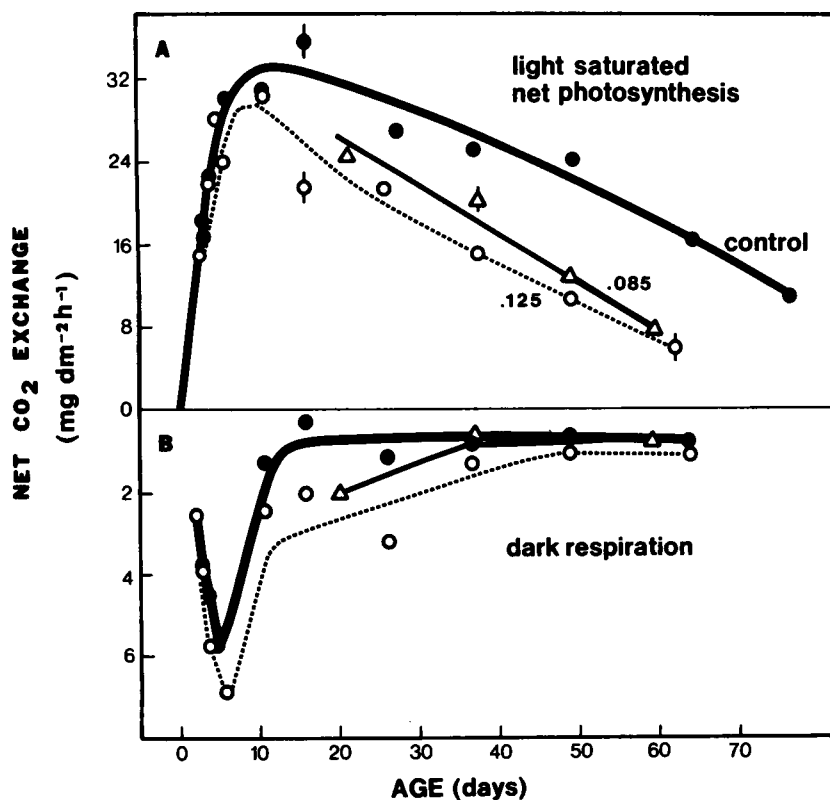


FIG. 1. Light-saturated net photosynthesis (A) and dark respiration (B) of variously aged hybrid poplar leaves chronically exposed to either 0.025 (●; control), 0.085 (Δ), or 0.125 (○) $\mu\text{l l}^{-1}$ ozone. All points are means (\pm SE) for at least three similarly aged leaves. Where SE bars are not shown, SE fall with the symbols. This applies to all figures.

processes. In expanding leaves (6 d old), response of P_n to light was basically similar in filtered air and O₃-treated leaves (Fig. 3). The only difference was a consistent (1–2 $\text{mg dm}^{-2} \text{h}^{-1}$) gap between the two treatments, probably due to higher dark respiration (Fig. 1) in the high O₃ treatment. As control leaves aged (from 24–58 d old), there was a gradual decline in the light saturation point and in P_n at that light level. In leaves of similar ages exposed to increasing concentrations of O₃, those declines were more rapid. Thus, the differences in light needed for saturation and in light-saturated or maximum P_n between control and O₃-treated leaves increased with increasing age. Also, differences in light-saturated P_n between control and O₃-treated leaves appear to be mostly due to photosaturation of O₃-treated leaves and not due to differences in the quantum yield efficiency of the photosynthetic systems.

Leaf Chl Contents and Relationship to P_n . Ozone treatment and leaf age had significant effects on leaf Chl contents (Fig. 4). Chl *a* contents reached a broad maxima at about 10 to 20 d in 0.125 $\mu\text{l l}^{-1}$ O₃-treated leaves and at 15 to 25 d in control leaves, and then declined—gradually in control leaves and more rapidly in leaves exposed to increasingly higher concentrations of O₃. Chl *b* contents in control leaves peaked at about 20 d and remained relatively stable with increasing age, while in O₃-treated leaves Chl *b* peaked at 10 d and declined thereafter. At all ages greater than 10 d, Chl *a* and/or *b* contents of ozone-treated leaves were always lower than in control leaves.

Total Chl (*a* + *b*) contents of similarly aged leaves were linearly related to light-saturated P_n , regardless of treatment (Fig. 5). Under controlled conditions, a high correlation has often been shown between the Chl content of leaves and CO₂ uptake (5, 6). This relationship changed with increasing leaf age, as light-saturated P_n apparently became less efficient per unit leaf Chl.

DISCUSSION

Exposure to low concentrations of O₃ had no immediate, direct effects on P_n , but chronic exposure to similar levels did have a number of effects on CO₂ exchange in hybrid poplar leaves. These included greater dark respiration rates in developing and young mature leaves and lower P_n in fully expanded leaves of all ages. The leaf maturation and aging processes themselves were well correlated with changes in CO₂ exchange. Age-related changes in P_n , R_D , light-saturation, leaf Chl contents, and apparent quantum yield were relatively typical and followed the pattern of increasing activity during maturation and gradual decline in subsequent aging. However, P_n and R_D rates were extremely high for tree species, and similar to levels observed in many crops. Also, hybrid poplar leaves were capable of sustaining high rates of photosynthesis for extended periods of time; over 50 d at $>20 \text{ mg dm}^{-2} \text{h}^{-1}$ and over 75 d at $>10 \text{ mg dm}^{-2} \text{h}^{-1}$.

Effects of exposure to low concentrations of O₃ were indicated by differences in age-related patterns of CO₂ exchange between control and ozone-treated plants. Until 7 d old, no differences in light-saturated P_n were observed between control and ozone-treated leaves, other than those due to differences in dark respiration. With increasing age, photosynthetic capacities and Chl contents of ozone-treated leaves declined more rapidly than in control leaves. Thus, although age-related patterns were similar for leaves in all treatments, they were accelerated in leaves exposed to O₃ and much of the decline in photosynthetic capacity of O₃-treated leaves was associated with this accelerated leaf aging. Longevity is significantly shorter for ozone-exposed leaves of hybrid poplar 207 (14, 15), and O₃ is generally known to accelerate leaf senescence (9, 12). Although chronic exposure to O₃ did not affect light-saturated P_n until leaves were greater than 10 d old, effects at low light levels (on apparent quantum yield) or in the dark (on R_D) were observed in leaves as young as 4 to

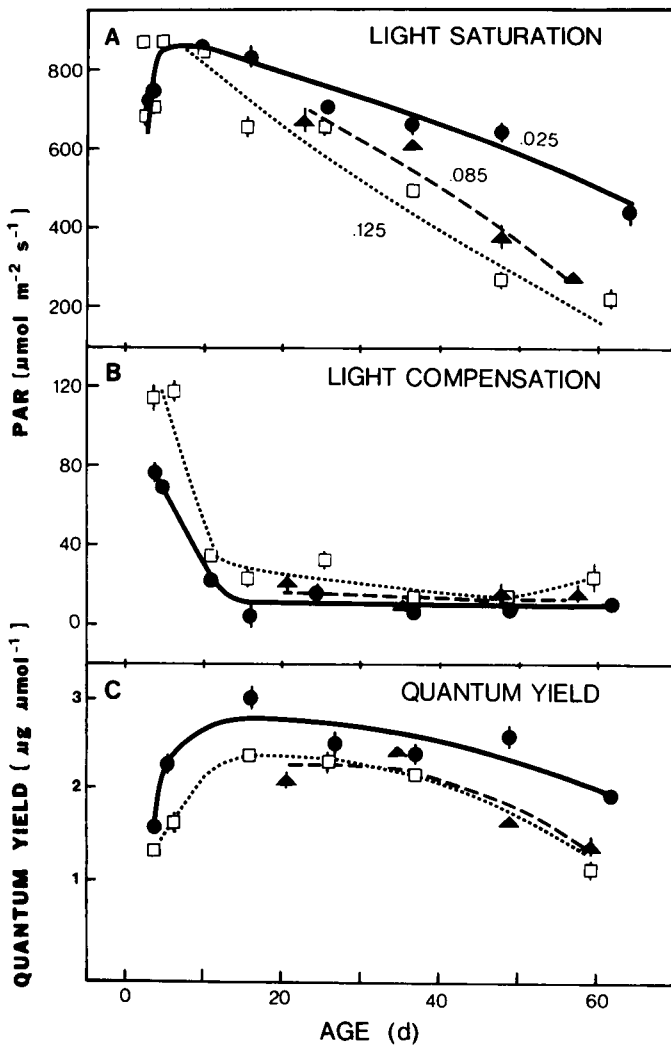


FIG. 2. Light saturation (A), light compensation (B), and apparent quantum yield (C) of variously aged hybrid poplar leaves chronically exposed to either 0.025 (●; control), 0.085 (▲), or 0.125 (□) $\mu\text{l l}^{-1}$ ozone; $n = 2$ or 3.

6 d old. Effects of O_3 exposure on R_p declined with increasing leaf age, and were minimal after leaves reached 35 d of age, while O_3 effects on P_n were greatest in older leaves. Thus, effects of O_3

on net photosynthesis and dark respiration were temporally unrelated, suggesting separate and distinct modes of action upon the mechanisms involved.

Other than accelerated leaf aging, what factors might have contributed to declining P_n in O_3 -treated plants? Although light-saturated P_n was linearly correlated with Chl content, the data do not allow us to determine whether there was any causal relationship, and it is possible that both P_n and leaf Chl were independently, but similarly, affected by O_3 treatments. What about potential indirect effects on P_n through stomatal perturbations? Extensive sampling of leaf diffusive conductance of leaves of all ages showed that the effects of O_3 on P_n were not due to O_3 -induced stomatal closure (14). For instance, depending on leaf age, O_3 -treated leaves had lower P_n but either lower or higher diffusive conductance than control leaves. Also, although O_3 exposure did not result in any discernible relationship between diffusive conductance and P_n , it did consistently reduce water use efficiency in leaves of all ages and at all light intensities (14). Thus, O_3 probably affects the photosynthetic process itself, in some combination of the following ways.

Ozone-treated plants had lower apparent quantum yields than control plants, suggesting that O_3 affects the photochemical reactions carried out by PSI and/or PSII. The effect was fairly constant over time, *i.e.* as leaves aged, the relative impact of O_3 on apparent quantum yield did not increase. In contrast, as leaves aged, light-saturated P_n of O_3 -treated leaves became increasingly reduced below P_n of control plants. Inasmuch as at light-saturating intensities neither photochemical reactions nor stomatal conductance (14) should be rate-limiting, chronic O_3 exposure probably influences the actual reduction of CO_2 , possibly by decreasing the content of RuBP-carboxylase, as has been found in alfalfa (13). In general, O_3 effects on CO_2 fixation could be either direct, or indirectly result from accelerated aging (due to O_3 disturbing general metabolic processes), or both. More research is needed before this question can be answered.

Decreases in net photosynthesis following chronic exposure to low concentrations of O_3 have been observed in a number of other species. Miller *et al.* (11) found significant declines in net photosynthesis of ponderosa pine seedlings treated for 60 d (9 h d^{-1}) at 0.15 $\mu\text{l l}^{-1}$ O_3 . In our laboratory, recent studies with sugar maple, red oak, and soybean chronically exposed to either 0.09 or 0.13 $\mu\text{l l}^{-1}$ O_3 found significant decreases in net photosynthesis (Reich, Schoettle, and Amundson, unpublished data). In contrast to the results with poplar, very young O_3 -treated soybean leaves showed immediate differences in P_n compared to controls, but never showed a difference in dark respiration. Perhaps increased dark respiration in poplar was due to increased maintenance

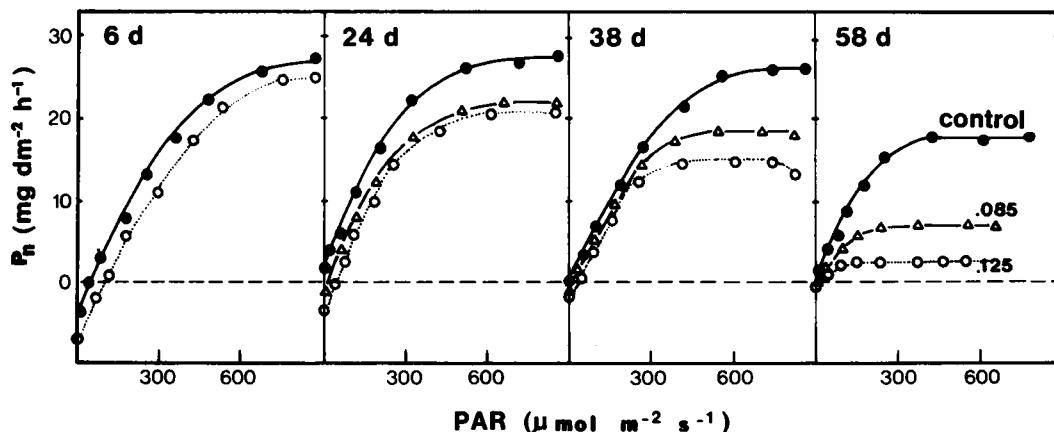


FIG. 3. Photosynthetic light response of variously aged hybrid poplar leaves chronically exposed to either 0.025 (●; control), 0.085 (▲), or 0.125 (○) $\mu\text{l l}^{-1}$ ozone. All curves represent mean values for two similarly aged leaves ± 1 SE.

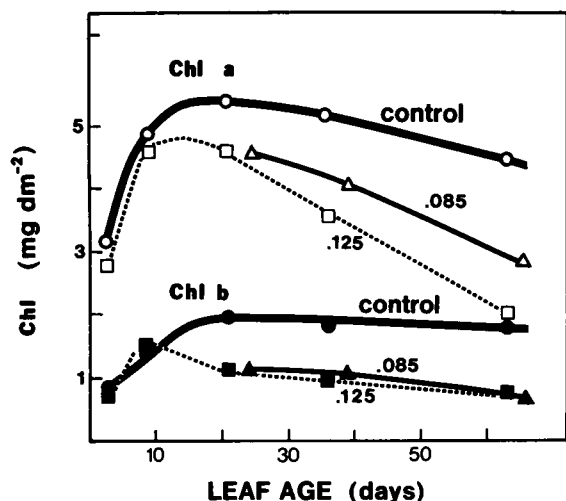


FIG. 4. Leaf Chl *a* (○, △, □) and *b* (●, ▲, ■) contents of variously aged hybrid poplar leaves chronically exposed to either 0.025 (○, ●; control), 0.085 (△, ▲), or 0.125 (□, ■) $\mu\text{l l}^{-1}$ ozone. Values are means for six replicate samples in each age and treatment class. All SE bars fell within the symbols and thus are not shown.

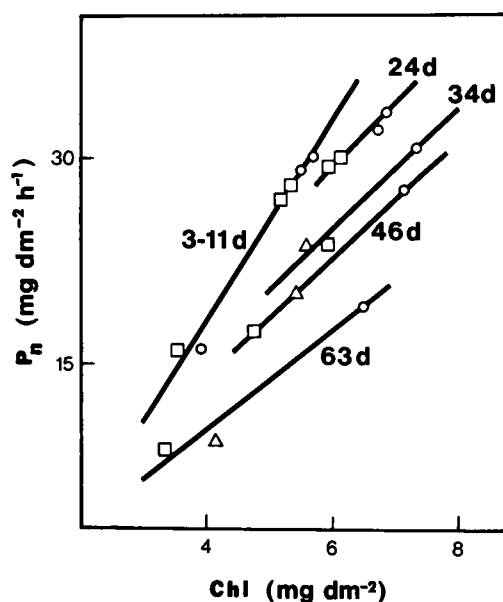


FIG. 5. Light-saturated net photosynthetic rates of leaves of various age classes in relation to leaf Chl *a* + *b* contents. Symbols are as in Figure 4.

which allowed ozone-treated leaves to maintain net photosynthesis rates similar to control leaves during much of the leaf maturation period.

Although no gas exchange work was done with poplar in the field, studies of growth and dry matter production using the same clone exposed to similar levels of ozone found similar, but greater, negative effects of O₃ exposure in the field than indoors (14). This was probably at least partially due to greater O₃ uptake rates by plants in the field, which had greater leaf diffusive conductances than plants grown indoors (14). Thus, results of this chamber study can probably be applied to plants grown in the field, especially since the greatest relative inhibition of P_n by O₃ was observed at the higher indoor light intensities, which were still only about one-third of full sunlight. Also, field studies in Europe and Japan (9, 12) with European hybrid poplar varieties support the results of this paper. Mooi (12) found accelerated

leaf aging in the Netherlands due to very low concentrations of O₃ (0.04 $\mu\text{l l}^{-1}$), and Kuno (9) observed significant reductions in net photosynthesis, leaf Chl contents, and growth due to ambient oxidant pollution near Tokyo, Japan. Finally, the results of this study underline the importance of examining the interacting effects of age and pollutant exposure upon whole leaf gas exchange. Without considering these interactions, any characterization of pollutant effects would be relatively incomplete.

CONCLUSIONS

The results of these experiments are important in view of the significant concentrations of O₃ in ambient air in most areas of the developed world. Other studies carried out with chronic, low levels of O₃ have found similar negative effects and the role of O₃ as an agent of accelerated aging is well documented. From this study, it is apparent that chronic exposure to low levels of O₃ places a stress on the photosynthetic and respiratory systems of hybrid poplar leaves, resulting in increased dark respiration and decreased leaf Chl contents and net photosynthesis. Apparently, accelerated leaf aging due to O₃ exposure was at least partially responsible for declining net photosynthetic capacity in such leaves. Also, the differential timing of the greatest effects of O₃ exposure on net photosynthesis versus dark respiration implies the existence of separate modes of action. The results of this study suggest that more emphasis needs to be placed on the environmental problem of low level oxidant pollution, and that more attention needs to be paid to the physiological response of plants chronically exposed to low levels of O₃.

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LITERATURE CITED

- ARNON DI 1949 Copper enzymes in isolated chloroplasts: polyphenoloxidase in isolated chloroplasts. *Plant Physiol* 24: 1-15
- CATSKY J, I TICHA, J SOLAROVA 1976 Ontogenetic changes in the internal limitations to bean-leaf photosynthesis. *Photosynthetica* 10: 394-402
- HORSMAN DC, AO NICHOLLS, DM CALDER 1980 Growth responses of *Dactylis glomerata*, *Lolium perenne* and *Phalaris aquatica* to chronic ozone exposure. *Aust J Plant Physiol* 7: 511-517
- HOWELL RK, EJ KOCH, LP ROSE JR 1979 Field assessment of air pollution-induced soybean yield losses. *Agron J* 71: 285-288
- KELLER T, J WEHRMANN 1963 CO₂-Assimilation, Wurzelatmung und Ertrag von Fichten- und Kiefern-samlingen bei unterschiedlicher Mineralstoffernahrung. *Mitt Schweiz Anst Forstl Versuchswes* 39: 217-242; cited in Kramer and Kozlowski 1979, p 218
- KRAMER PJ, TT KOZLOWSKI 1979 *Physiology of Woody Plants*. Academic Press, New York
- KRESS LW 1980 Effect of O₃ and O₃ + NO₂ on growth of tree seedlings. In *Proceedings of Symposium on Effects of Air Pollutants on Mediterranean and Temperate Forest Ecosystems*, June 1980, Riverside, CA. General Technical Report, Pacific Southwest Forest and Range Experiment Station, U. S. Forest Service, Berkeley, CA
- KRIEDEMANN PE, WM KLIWEYER, JM HARRIS 1970 Leaf age and photosynthesis in *Vitis vinifera* L. *Vitis* 9: 97-104
- KUNO H 1980 Effects of photochemical oxidant on the growth of poplar cuttings. II. Effects of photochemical oxidant on chlorophyll contents, photosynthetic and dark respiratory rates, soluble carbohydrate and nitrogen contents in leaves of different ages. *Taiki Osen Gakkaishi* 15: 155-162
- LUGG DG, TR SINCLAIR 1981 Seasonal changes in photosynthesis of field-grown soybean leaflets. I. Relation to leaflet dimensions. *Photosynthetica* 15: 129-137
- MILLER PR, JR PARMETER JR, BH FLICK, CW MARTINEZ 1969 Ozone dosage response of ponderosa pine seedlings. *J Air Pollut Control Assoc* 19: 435-438
- MOOI J 1980 Influence of ozone on growth of two poplar cultivars. *Plant Disease* 64: 772-773
- PELL EJ, NS PEARSON 1982 Quantity of RuBP-carboxylase in three cultivars of alfalfa stressed by O₃. *Phytopathology* 73: 372
- REICH PB 1983 Effects of low levels of O₃ and SO₂ on growth and physiology of hybrid poplar and soybean. PhD thesis. Cornell University
- REICH PB, JP LASSOIE 1981 Effects of O₃ and SO₂ on growth of hybrid poplar.

- Plant Physiol 67: S-18
16. REICH PB, RG AMUNDSON, JP LASOIE 1982 Reduction in soybean yield after exposure to ozone and sulfur dioxide using a linear gradient exposure technique. *Water Air Soil Pollut* 17: 29-36
 17. WILHOOR RG, GE NEELY 1977 Growth response of conifer seedlings to low ozone concentrations. *In* International Conference on Photochemical Oxidant Pollution and Its Control. United States Environmental Protection Agency Ecological Research Series 600/3-77/00 1b, pp 635-645